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preirradiation ecological studies

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The Enterprise, Wisconsin, Radiation Forest

Preirradiation Ecological Studies

Thomas D. Rudolph
Editor

Institute of Forest Genetics
North Central Forest Experiment Station
Forest Service, U. S. Department of Agriculture
Rhinelander, Wisconsin

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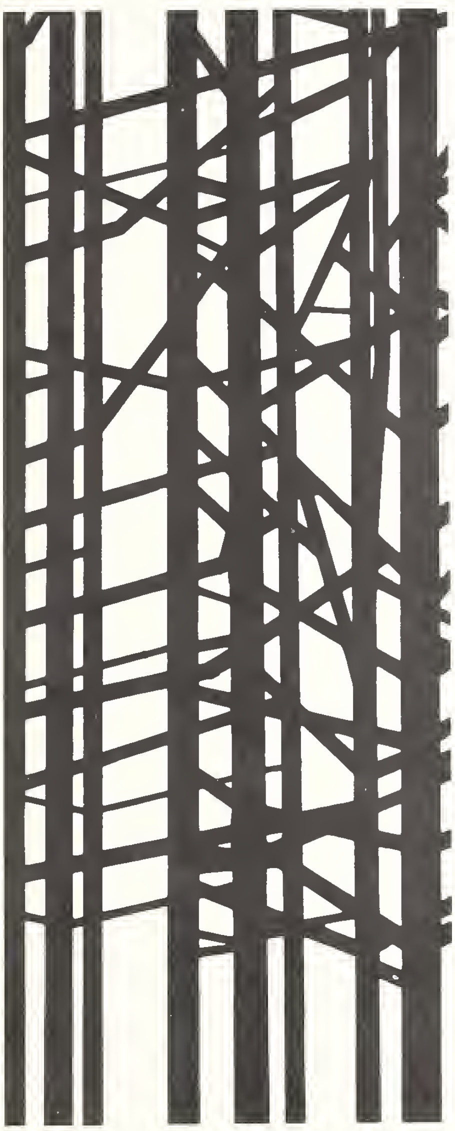
Preface



The research on which the papers in this volume are based is an expansion of radiation studies begun at the Institute of Forest Genetics in 1961. The earlier research was primarily concerned with gamma field and laboratory studies of responses of individual tree species to gamma radiation. In 1968 the research program was expanded to include investigation of responses to massive dosages of gamma radiation in natural northern forest communities of the Enterprise Radiation Forest near Rhinelander, Wis. The information to be obtained would complement radioecological results obtained in studies of other types of forests, such as those on Long Island and in Puerto Rico. Since 1968 this radioecology research has represented a cooperative effort between the U. S. Atomic Energy Commission, Division of Biomedical and Environmental Research, and the U. S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, of which the Institute of Forest Genetics at Rhinelander is a part. During these years the major portion of the financial support for the research has been provided by the Atomic Energy Commission.

Plans were developed for a research program to extend over a 20-year period and to include irradiation of various northern forest types during different seasons of the year, as well as a 5-year exposure of one of the major northern forest types, namely, aspen. The papers in this volume are concerned with preirradiation studies on the first site chosen for irradiation. They present results of field studies conducted from 1968 through early 1972 by the project staff and a number of cooperators from nearby universities. The fairly broad range of ecological studies included was limited only by the available research staff and financial support for cooperators.

The information contained in this volume is largely descriptive of the physical and biological environments of the Enterprise Radiation Forest and is intended to supply reference and base-line information not only for evaluating the gamma-radiation impact but also on the ecology of some important northern forest types.

The first two chapters describe the Enterprise Radiation Forest in general, its development into a research facility, and the overall experimental design for the first site to be irradiated and the control area.

The third chapter summarizes solar radiation measurements made both in the open and under the tree canopies in the forest communities of the first site and the control area.

The next five chapters deal primarily with descriptions of the vegetation composing the forest communities under study in the Enterprise Forest. Included is a consideration of the lichens, ground vegetation, shrub layer, and tree cover.

Chapters 9 and 10 are concerned with litter production in the first radiation site and the control area. Chapter 10 examines leaf-litter production by individual tree species.

Chapters 11 and 12 describe the vertebrates of the Enterprise Forest and include a general survey of species found in the entire forest as well as more detailed information on small-mammal populations in the first study areas.

In the final chapter, we attempt to predict the impact of irradiation during one growing season on the communities of the first site and on the species composing these communities. The predictions, based primarily on nuclear parameters of the plant species, will be compared with the responses observed following irradiation.

The first site was irradiated during the 1972 growing season. Observations and measurements of the impact of radiation on the communities and the progress of the communities toward recovery are continuing.

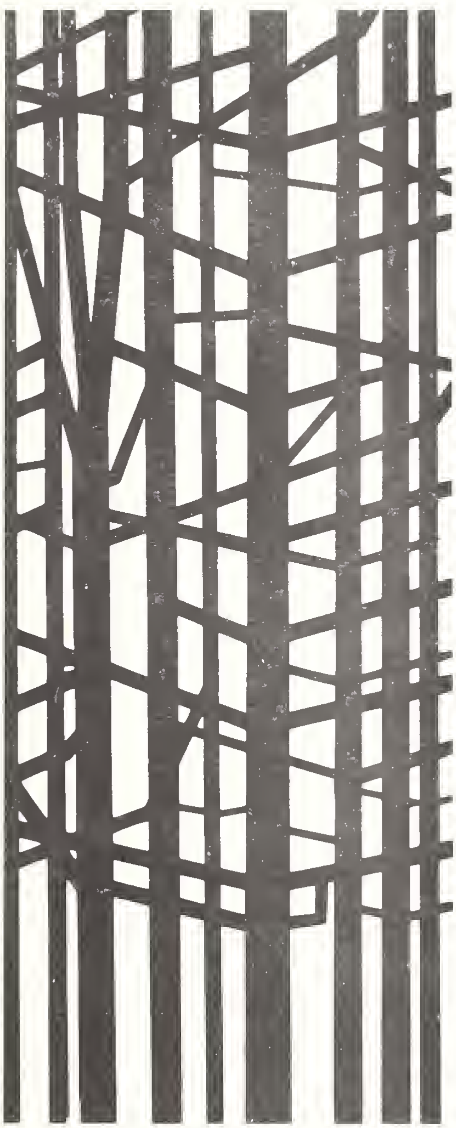
Recently, because of changing priorities within the Atomic Energy Commission, the decision was made to terminate AEC support of this research. Without this support the Forest Service is not able to continue the research. Therefore, the project will be officially terminated as of June 30, 1974. As much as possible of the research results from the irradiated site and the control area will be summarized by the project staff before that time. These results will be published in the open literature, primarily in appropriate scientific journals. The individual journal articles will eventually be brought together and published as a companion volume on the Enterprise Radiation Forest by the AEC. Pertinent addenda and appendixes will be added in the companion volume to provide more detailed information than can be presented in individual journal articles.

The information in this volume and in the future publications will be a valuable addition to the ecological, particularly the radioecological, literature and will be useful not only to interested scientists but to all persons concerned with the management of our northern forest resources.

Thomas D. Rudolph
Editor

March 1974

Contents



The Enterprise Radiation Forest Research Facility

T. D. RUDOLPH
Institute of Forest Genetics, North Central Forest Experiment Station, Forest Service, U. S. Department of Agriculture, Rhinelander, Wisconsin

ABSTRACT

A 1440-acre forest in northern Wisconsin which is being used for gamma-irradiation studies on various northern forest communities is described. A brief history of the area, which is typical of much of the upper Great Lakes forest region, is presented together with a description of its current condition. Development of the tract into a radiation research facility is described. A 10,000-Ci ^{137}Cs radiation source was used. Studies on each radiation site will include characterization of the preirradiation communities, changes occurring during irradiation, and postirradiation recovery.

Research on the effects of ionizing radiation on various terrestrial ecosystems has been under way for well over a decade. Major facilities developed for radiation research on plant communities and their individual components include those at Emory University (Platt, 1962), Brookhaven National Laboratory (Woodwell, 1963), Savannah River, Georgia (Golley and McCormick, 1966), and the Nevada Test Site (French, 1964) and in Puerto Rico (Odum and Pigeon, 1970). Since 1965 we have used ^{137}Cs point sources at our institute to study radiation effects on individual forest tree species (Rudolph, 1964; Miksche and Rudolph, 1968; Rudolph and Miksche, 1970). Although the northern forests of coniferous and deciduous species cover a large portion of the landscape from Nova Scotia to Connecticut and westward into the northern Lake States and adjoining areas of Canada, little is known about the effects of ionizing radiation on these intact ecosystems.

Over this vast area the forests grade into primarily deciduous species composition southward and toward pure boreal coniferous forest to the north. Although the numerous forest types include a wide variety of understory and animal species, some similarity in composition and successional patterns exists over the entire northern forest area. Interspersed throughout the forests and especially uniform in structure and composition are the bogs that cover a significant portion of the area, together with muskegs and open aquatic communities.

In the Lake States region, which includes northern Wisconsin, the major components of northern forest communities are stands of white spruce–balsam fir; lowland conifers; hemlock; aspen–birch interspersed with red, white, or jack pine; and assorted hardwood species, which occur where soil and climatic conditions are favorable and where disturbance is not recent and thus allows succession to proceed to more stable climax species. This forest area, therefore, is composed of a series of communities intergrading both in time and in space. Compared with the complexity of the Puerto Rican rain forest (Odum and Pigeon, 1970), the communities are relatively simple in tree-species composition and successional pattern, but they are more complex than the pine–oak forest of Long Island, New York (Woodwell and Sparrow, 1963). Both the rain forest and the pine–oak forest have been the subjects of radioecological studies. The northern forests can be drastically changed by natural and man-caused catastrophic events or environmental stresses, including, among others, fire, unusually severe weather conditions, insect and disease epidemics, and timber harvesting. Undoubtedly gamma radiation will also change these forests drastically, depending on the exposure level and perhaps on the season of the year during which the forest is exposed.

It is the purpose of the research in the Enterprise Radiation Forest to determine the impact of gamma irradiation during various seasons of the year on intact natural northern forest communities and on the components of those communities. Studies of recovery of the communities from the radiation stress and comparison with other man-caused or natural disturbance factors will also be important aspects of research.

The material presented in this volume contains considerable ecological information from a forest site monitored intensively before irradiation. This first chapter provides background information on the Enterprise Forest area and describes how and why the area was selected and its development into a radiation research facility. This information is intended to serve as a common base for the diverse subject matter in subsequent chapters pertaining to the experimental site.

The preirradiation conditions in the northern forest communities irradiated in Enterprise Radiation Forest site 1 are described in the succeeding chapters, together with the experimental designs applied to the study of the communities.

SELECTION OF THE RESEARCH AREA

Early in 1967 the U. S. Atomic Energy Commission inquired as to our interest in expanding our existing radiation research on individual forest tree species to include investigations of seasonal irradiation effects in natural northern forest communities. After a meeting in Rhinelander between representatives of the AEC and the Institute of Forest

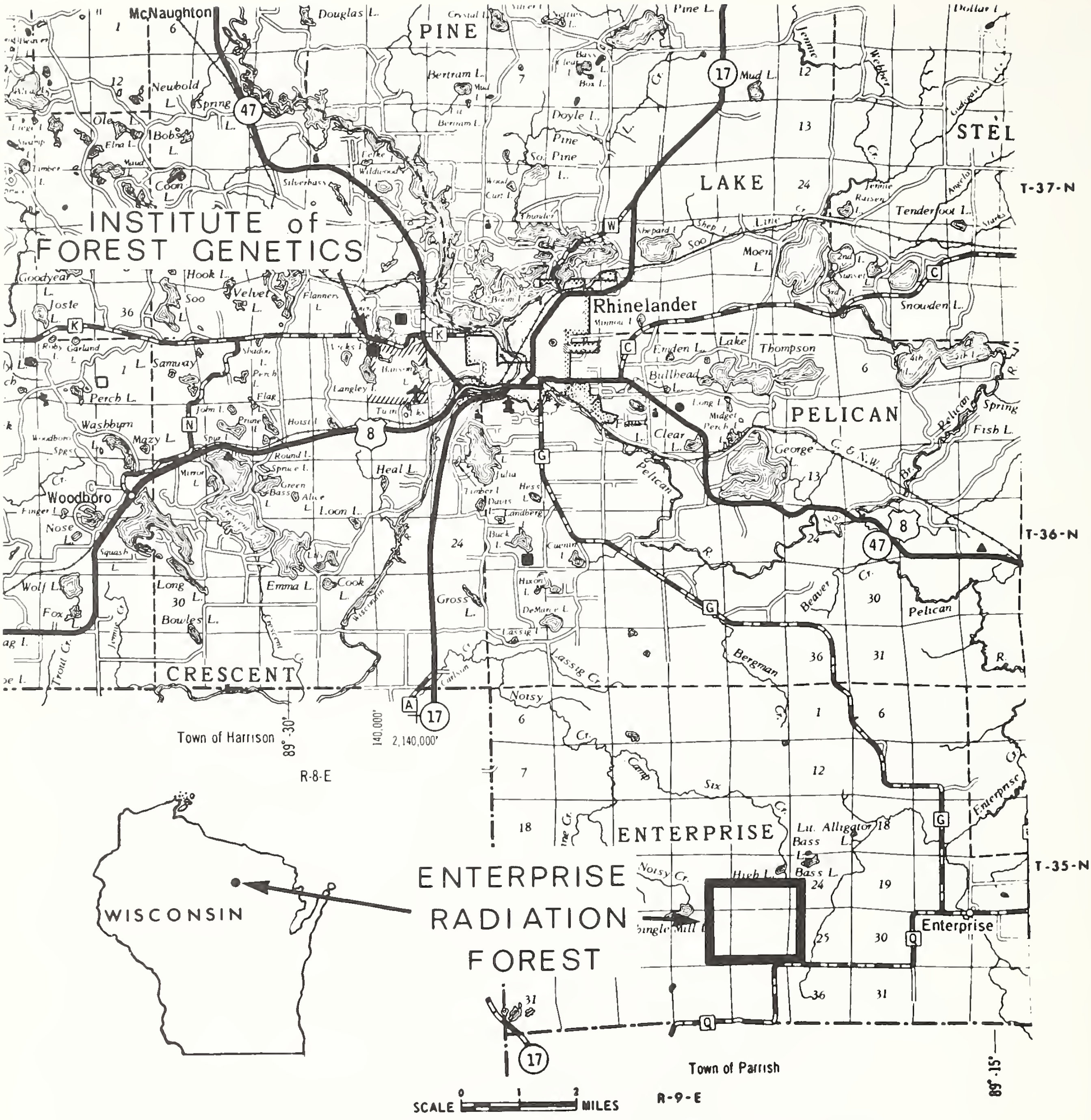


Fig. 1 Portion of Oneida County map showing location of Enterprise Radiation Forest.

Genetics to discuss the feasibility of such research at the institute, a preliminary proposal outlining general plans for the research was prepared by Hans Nienstaedt, J. P. Miksche, Forest Stearns, and T. D. Rudolph in June 1967. This proposal, which was approved by the Forest Service and the AEC, included the following criteria to be used in selecting a radiation research area: (1) The area must be within no more than 30 min driving time from the Institute of Forest Genetics near Rhinelander. (2) It must be in a contiguous block and in public ownership. (3) The size of the area must be adequate to provide for at least five separate radiation sites. (4) The location should be remote from human habitation. (5) Flora and fauna typical of northern forests must be present in the area to meet the radioecological research needs. (6) The topography must not be extreme.

With these criteria as guides, we began a search for potential areas suitable for the planned natural-forest radiation studies. Several possible sites were chosen for review and consideration by a group of thirteen scientists from the United States and Canada who are qualified and experienced in radiobiological research. The group met in Rhinelander in March 1968 to review and inspect the sites and subsequently recommended the Enterprise area (Fig. 1) near Rhinelander (45°30′ north latitude and 89°20′ west longitude) as the best available for the research program.

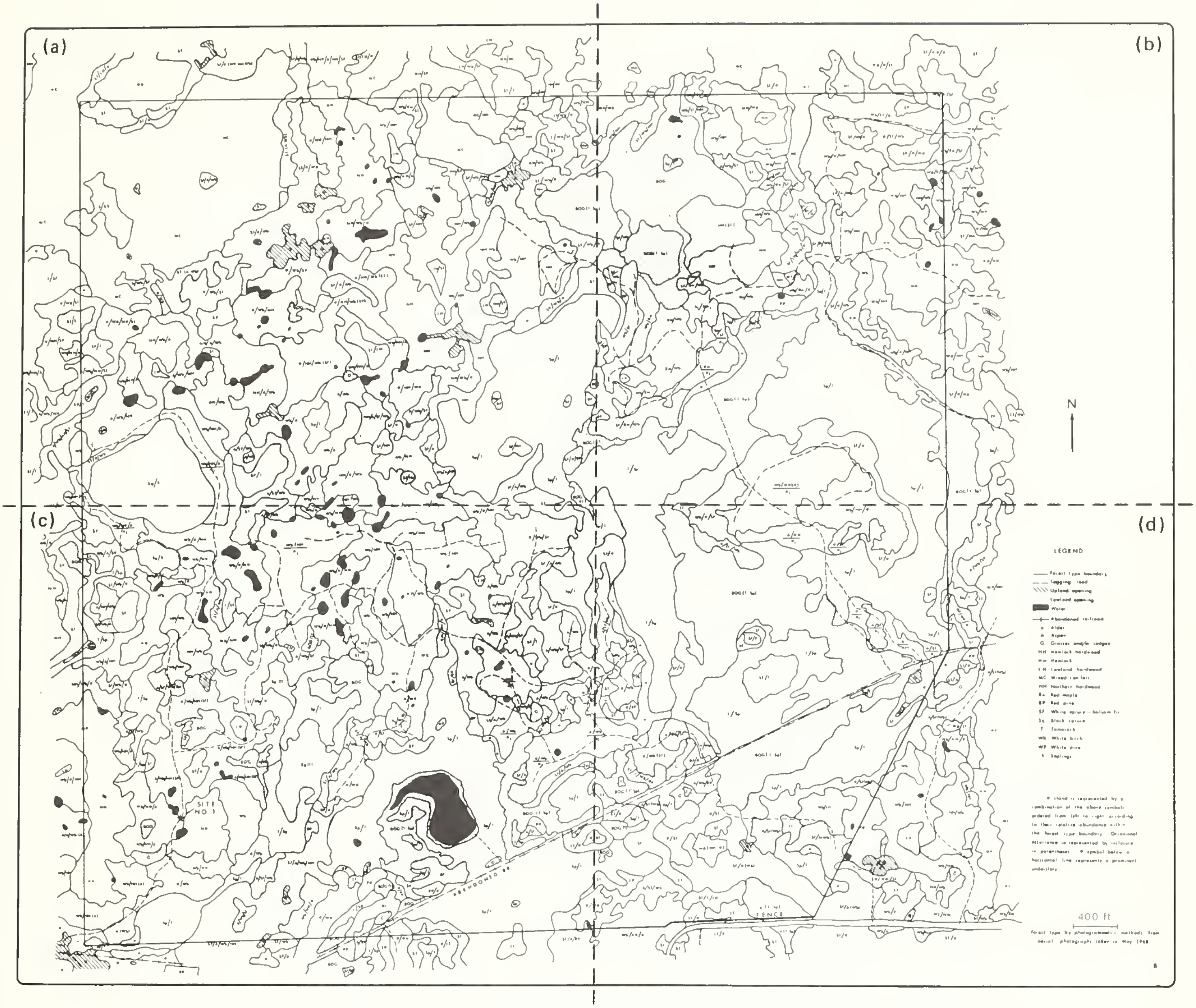


Fig. 2 Forest-type map of the Enterprise Radiation Forest. Enlarged views of sections a to d appear on pp. 4 to 7.

The logging and fire history of the area since the turn of the century is similar to that of most of the Lake States forest area. It was initially cut over between 1910 and 1914, and the logs were shipped to sawmills in surrounding areas on a railroad that passed through the southeastern portion of the present experimental area (Figs. 2 and 3). The railroad was abandoned and removed in 1950. Indications are that, before logging, most of the upland sites were covered with large white and red pine and northern hardwoods. In the decade that followed the initial logging, most of the area reverted to public ownership through tax forfeit. Fires were common in the cut-over areas, and all the present experimental area (with the possible exception of some of the wet lowlands) burned over at least once before 1926. In 1926 forest-fire protection of the area was assumed by the State of Wisconsin, and no major fires have occurred in the past 40 years. Thus most of the trees composing the present forest stands in the area originated since 1926. Scattered older individuals and groups which were too small for sawtimber at the time of initial logging and which survived subsequent fires also are found. Some of these remnants of the early logging, plus some of the older second-growth stands, have been harvested since about 1950, primarily for pulpwood, in small areas within the forest. No cutting has occurred since 1968. Thus the area is representative of much of the north central North American forest region dominated by second-growth seral types resulting from logging and subsequent fire disturbances.*

Oneida County owned 1160 acres of the proposed tract, and the State of Wisconsin owned 280 acres. The portion

*Much of the information on the disturbance history of the Enterprise Forest was obtained in personal communication with Arthur Buelow, Enterprise, Wisconsin, a resident of the area since the time of the initial logging.

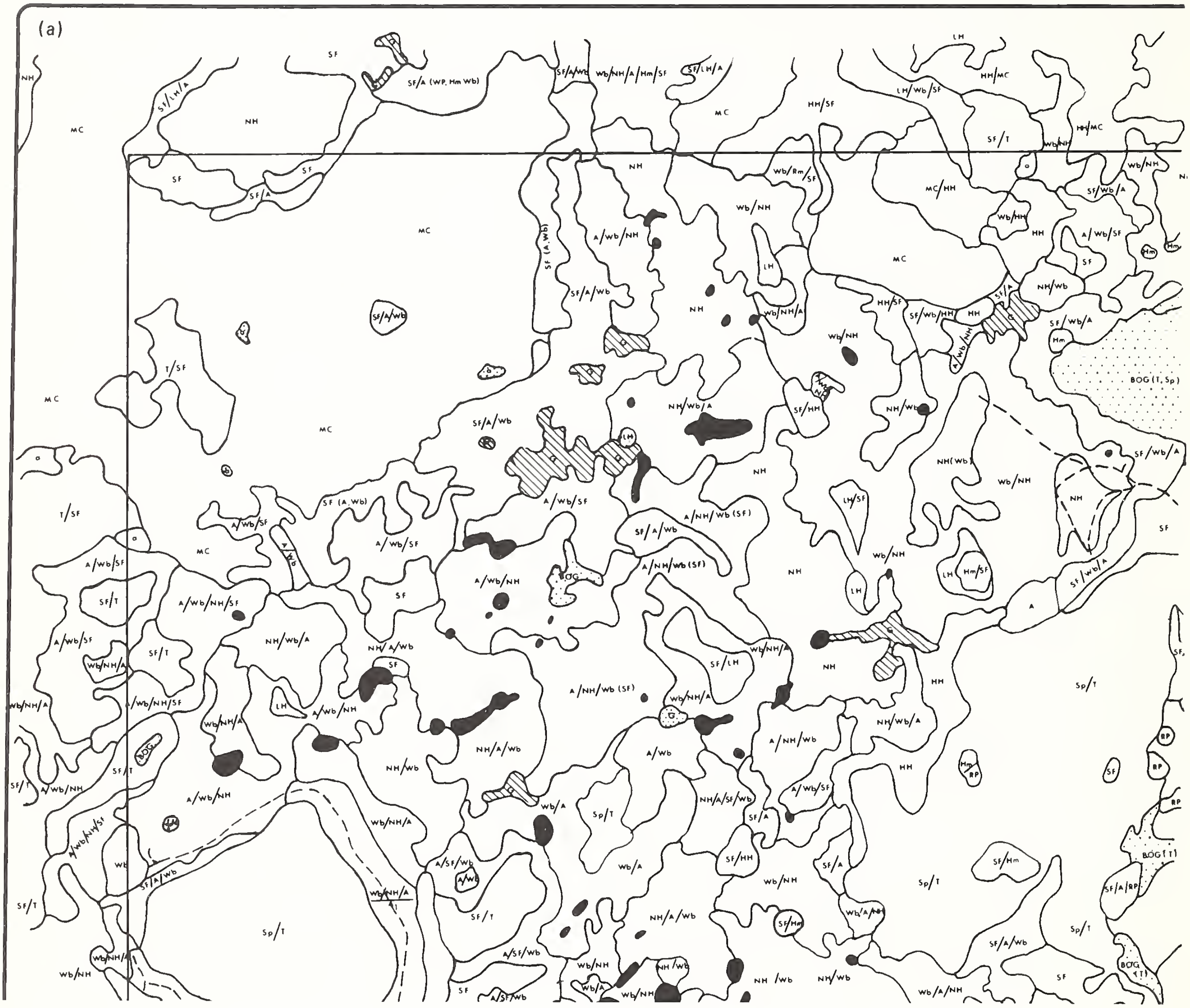


Fig. 2a Enlargement of upper left quadrant of forest-type map.

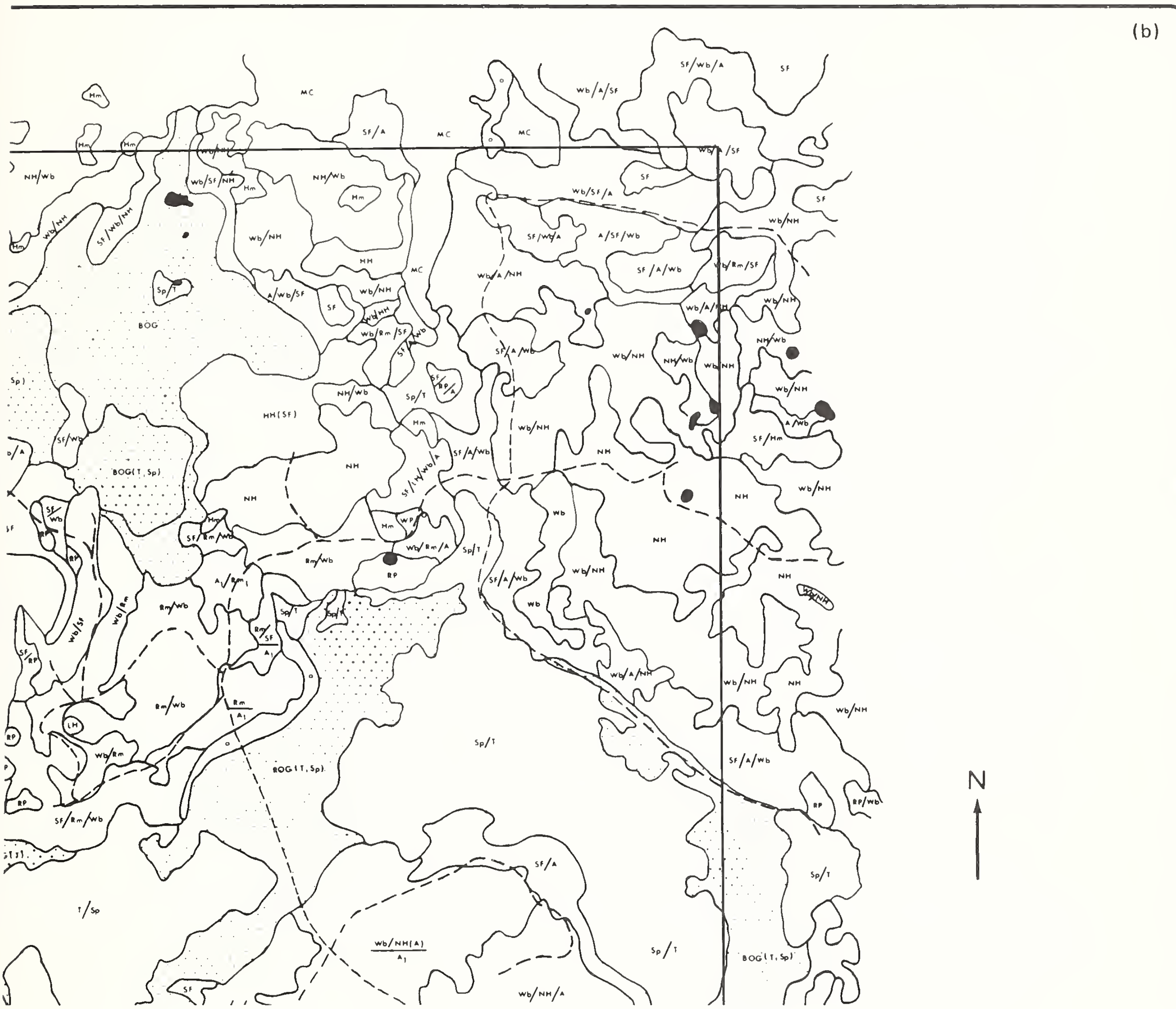


Fig. 2b Enlargement of upper right quadrant of forest-type map.

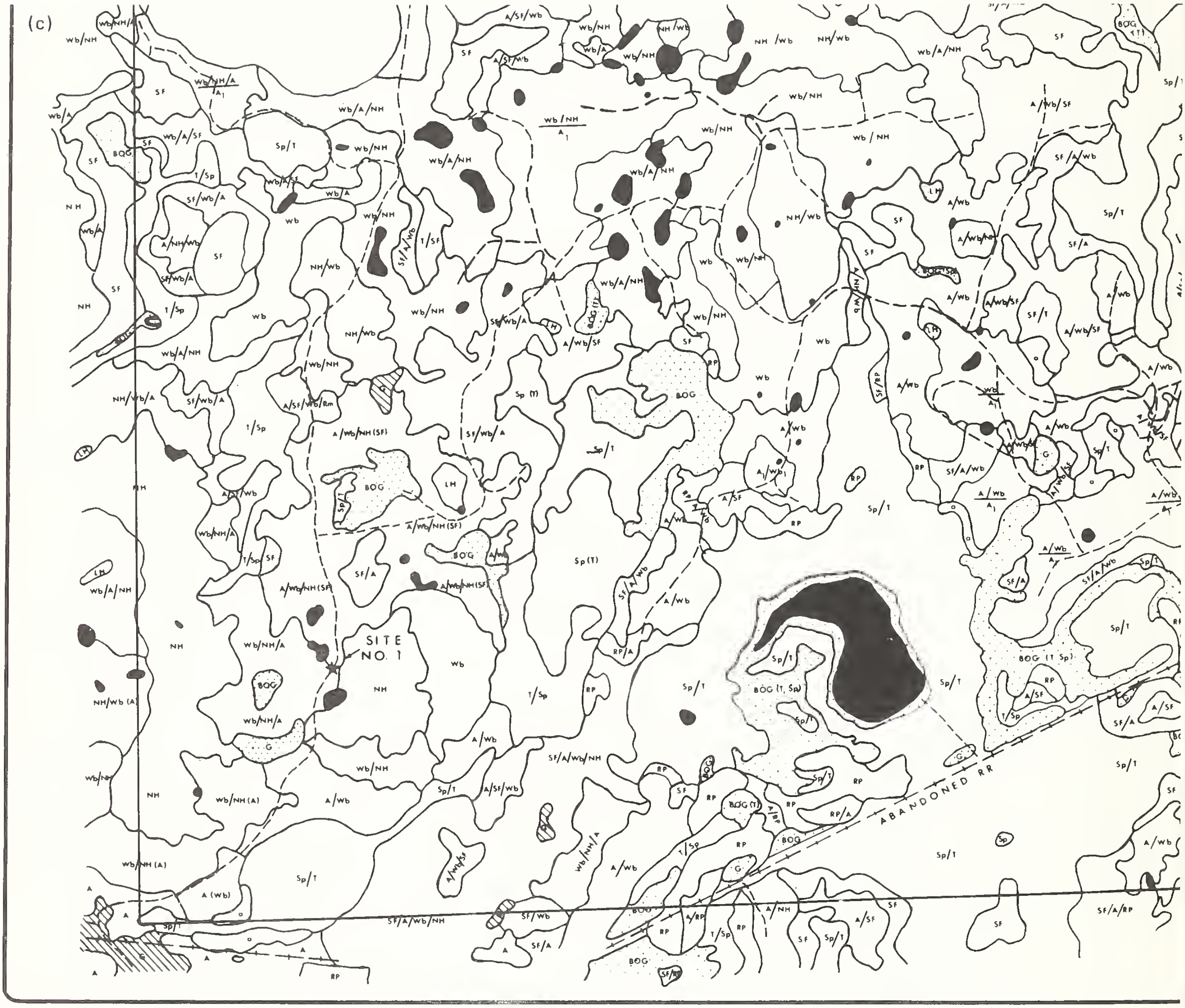


Fig. 2c Enlargement of lower left quadrant of forest-type map.

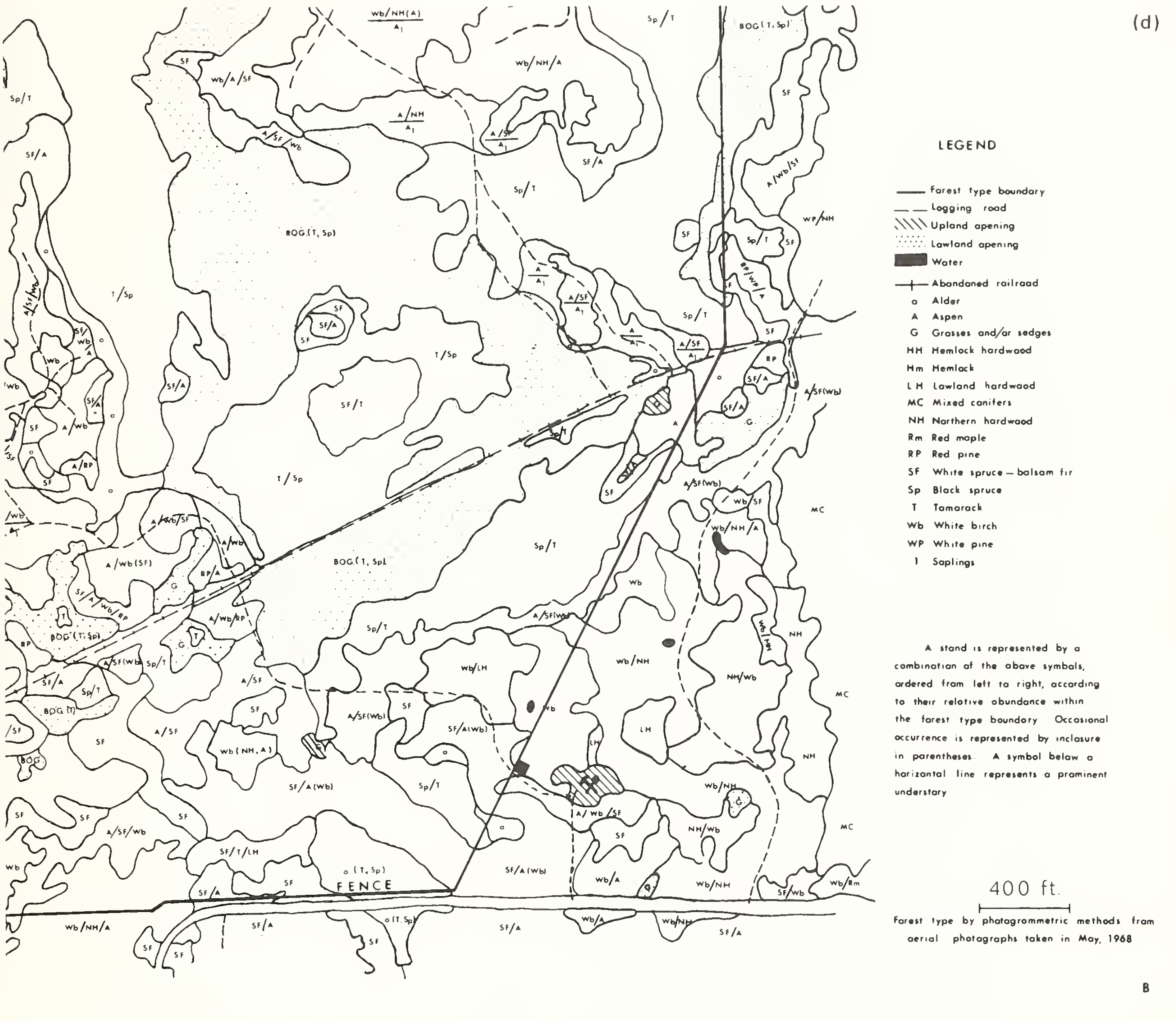


Fig. 2d Enlargement of lower right quadrant of forest-type map.

of this area in State of Wisconsin ownership was subsequently purchased by Oneida County. The U. S. Forest Service leased the entire tract from Oneida County for 20 years beginning Aug. 1, 1969, for a fee of $8476, with an option to renew.

DEVELOPMENT OF THE ENTERPRISE FOREST INTO A RESEARCH FACILITY

Boundary Survey and Aerial Mapping of Area

After the lease arrangement with Oneida County was completed, the boundary of the area was surveyed by the Engineering Division of the Nicolet National Forest.

Aerial photographs of the area were taken in May 1968, and a detailed forest-type map (Fig. 2) and a contour map (Fig. 3) were prepared from the photos. The forest-type map shows the complexity of the forest cover and clearly indicates the second-growth nature of the stands. The contour map illustrates the undulating topography but also shows that the maximum and minimum elevations over the entire area differ by only about 27 m.

Soil Survey

A soil survey of the area was made under contract by the U. S. Soil Conservation Service, and a soil-type map was prepared by Harvey V. Strelow of that agency (Fig. 4). A description of the soil types is given in Table 1. Much of the area contains Couderay peat soils, and the remainder is overlaid with loams and silt loams. The diversity of the forest types found in the area reflects the variety of soils present. Their potential for forest production ranges from poor on the peat soils to good on the silt loams and loams.

Selection of Radiation Site 1 and Preirradiation Studies

A reconnaissance survey of the Enterprise Radiation Forest was made during the summer of 1969 to evaluate and select specific sites for irradiation. Preliminary vegetation surveys were made on a number of potential exposure sites. An estimate of the species composition and density was obtained on tree, shrub, and ground vegetation. These preliminary surveys formed the basis for the selection of the first site to be irradiated. The selected site was at the junction of three forest types—aspen, paper birch, and northern hardwood—as typed from the aerial photographs (Fig. 2). These three types represent important components of typical ecosystems occupying vast areas within the northern forest.

A control area was established for each of the three forest types at an adequate distance from the radiation source to prevent radiation damage. Selection of both treatment and control areas was necessarily subjective, and, in addition to species composition and density, factors of safety, accessibility, availability, and economy were considered. A more detailed description of these stands is found in Chap. 6.

Specific research on radiation site 1 being carried on by the project staff deals with (1) primary productivity, (2) litter fall and accumulation, (3) seed production of northern forest species, (4) composition and structure, (5) phenology, (6) wild, small mammal populations, and (7) microenvironment. Available preirradiation results of these studies are presented in this volume.

Studies being carried on by cooperators from other institutions include (1) population dynamics of large-leaved aster and bunchberry, (2) response of a forest ecotone to ionizing radiation, (3) carbohydrate concentration in radiation-stressed trees, (4) effects of radiation on lichens and lichen-forming fungi and algae, and (5) the effects of gamma radiation on black knot on black cherry and *Eutypella* canker on red maple.

Security Fence

A security fence (Fig. 5) surrounding the 583-ha (1440-acre) Enterprise Radiation Forest was completed in May 1971. The fence is a 2.4-m- (8-ft-) high chain-link fabric topped with six barbed wires, three on each side of a V-shaped arm. It is inspected periodically for damage, such as from falling trees, large burrowing animals, vandals, and other agents. The fence is constructed in the center of a 20-m- (66-ft-) wide clearing, and areas along the fence which are subject to erosion have been sown with a grass–clover mixture to stabilize the soil.

Standard "Caution—Radiation Area" signs are posted at 30-m (100-ft) intervals on the fence. Similarly, "Wisconsin Wildlife Refuge" signs indicate that no hunting or trapping is permitted within the area.

The fence has proved to be an effective barrier to the ingress of deer, but small mammals move freely through the fabric.

A gate near the control building is the only opening in the fence (Fig. 5). The gate lock is electrically interlocked with the radiation-source controls and switches off electrical power to the radiation source when the gate is opened.

Radiation-Source-Control Building

A building to house the radiation-source controls and related equipment was constructed near the southeast corner of the forest about 200 m off Oneida County Highway Q (Fig. 5). It is a 6.7- by 8.5-m (22- by 28-ft) concrete-block building with wooden partitions and includes a room for the radiation-source controls and two-way radio, a small office–field laboratory, a one-stall garage and storage area, and a toilet.

Entrance into the fenced radiation forest must be through this building. A worker can open the electrical lock on the gate only from inside the fence after he has passed through the control building. An electrical switch on the control-building door opening into the radiation forest and the electrical lock on the gate both discontinue power to the radiation source when the door or the gate is opened. Power cutoff causes the radiation source to fall into a lead shielding cask and renders the area safe for entry even though normal procedures for lowering the source before the door or gate is opened may have been by-passed.

The Radiation Source

The gamma-radiation source used in the Puerto Rico Rain Forest studies at El Verde (Odum and Drewry, 1970) was transported by ship in a Sugarman Impact Container from Puerto Rico to Jacksonville, Fla., and then by motor freight to the Oak Ridge National Laboratory where it was reencapsulated with 10,000 Ci of ^{137}Cs on Aug. 18, 1971. Total weight of the isotope was 416.7 g, and activity was 24.0 Ci/g. The source was then reinstalled in the lead cask, and the cask was reloaded into the container and shipped by motor freight to Rhinelander.

The source arrived in Rhinelander on Sept. 3, 1971, and was temporarily stored in the cultivated gamma-radiation field at

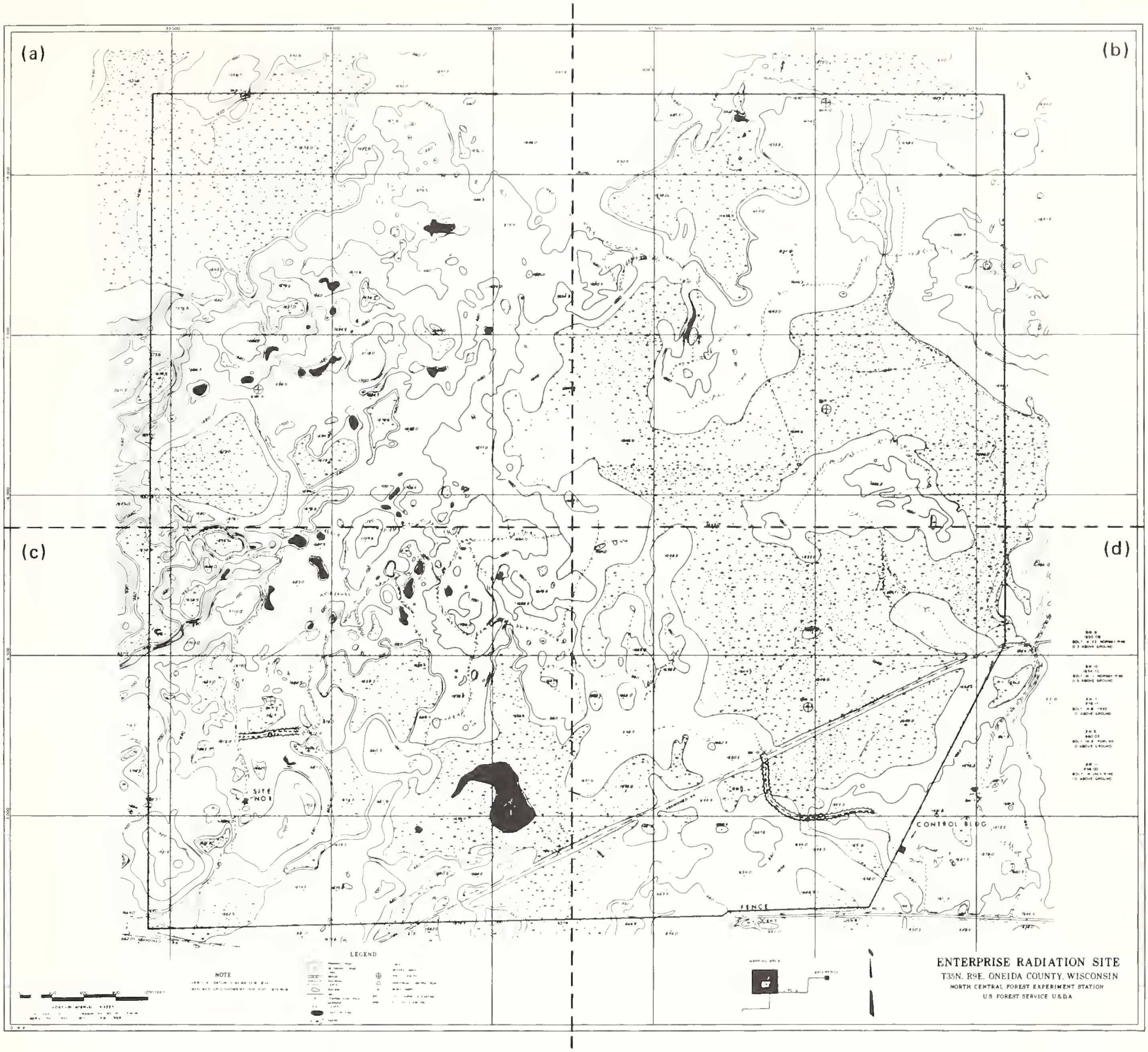


Fig. 3 Contour map of the Enterprise Radiation Forest. Enlarged views of sections a to d appear on pp. 10 to 13.

the institute until it could be moved to the Enterprise Radiation Forest. A truck with jointed boom and hoist used for handling palleted concrete blocks was rented to load, transport, and unload the source in the Enterprise Forest. The source was placed in position in radiation site 1 (Fig. 6) atop a 1.8- by 1.8-m (6- by 6-ft) wooden platform 1.8 m (6 ft) above the ground. The platform is supported by nine 15- by 15-cm (6- by 6-in.) wood posts sunk 1.2 m (4 ft) into the ground. The floor of the platform is supported by 5- by 15-cm (2- by 6-in.) joists and is made of 2.5-cm (1-in.) marine plywood topped with a 1.8- by 1.8-m by 1.25-cm (6- by 6-ft by ½-in.) steel plate.

With the assistance of James Wilde of the Oak Ridge National Laboratory, we installed the elevator guide tube and other mechanical components of the irradiator in late autumn of 1971.

When the control building was completed and the electrical powerline to the building site was constructed, the necessary electrical cables were placed on the ground along the access road from the building to the radiation source at site 1. The distance along this route is approximately 3350 m (11,000 ft).

Because the long length of the ground-laid electrical cables resulted in substantial decreases in voltage at the source, and because the control system needed to have a programmed mode of operation added, considerable modification was necessary both at the source and in the components in the control building.

An emergency trip cable for unhooking the lead plug and source capsule was installed and extended to a distance

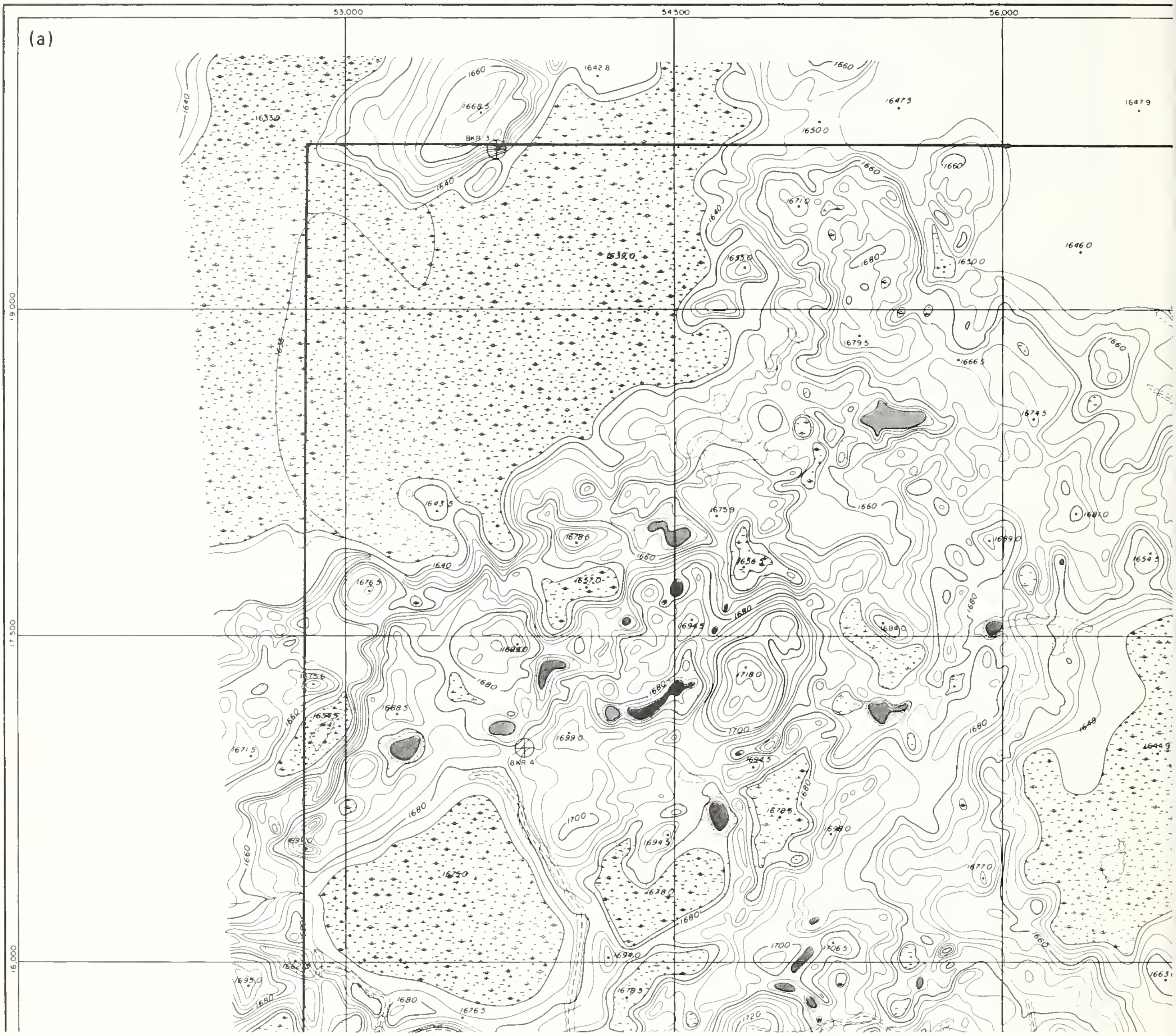


Fig. 3a Enlargement of upper left quadrant of contour map.

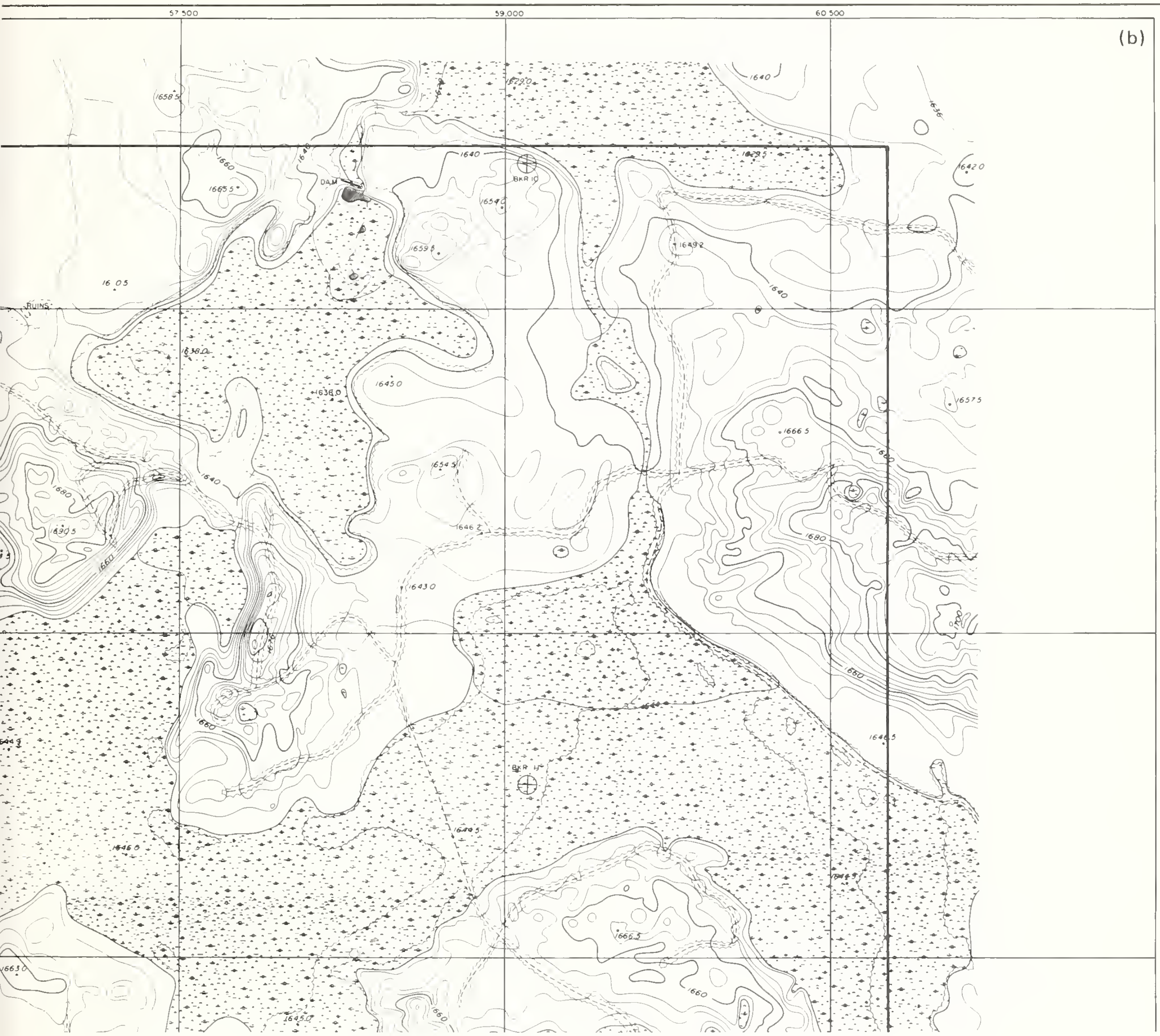


Fig. 3b Enlargement of upper right quadrant of contour map.

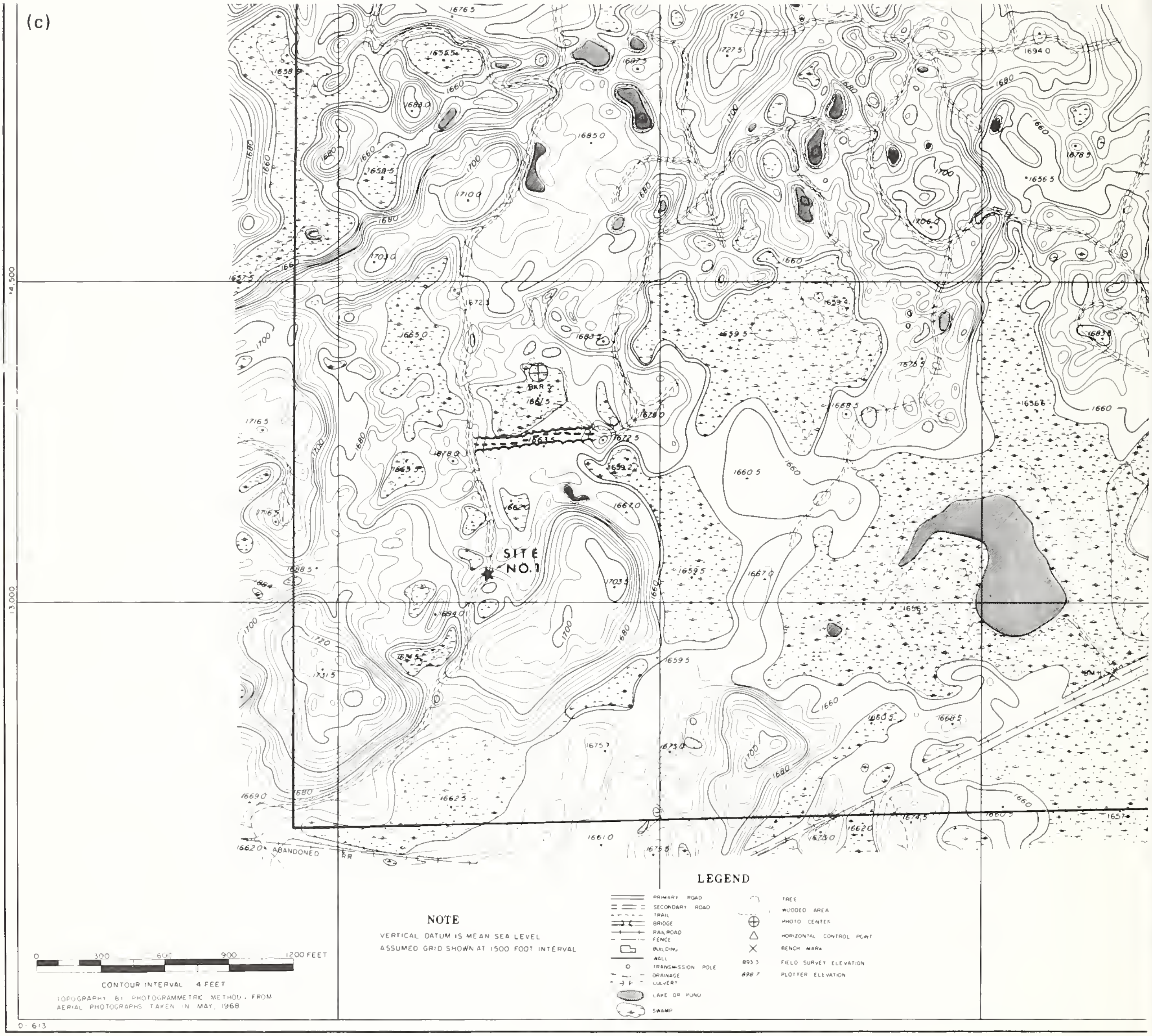


Fig. 3c Enlargement of lower left quadrant of contour map.

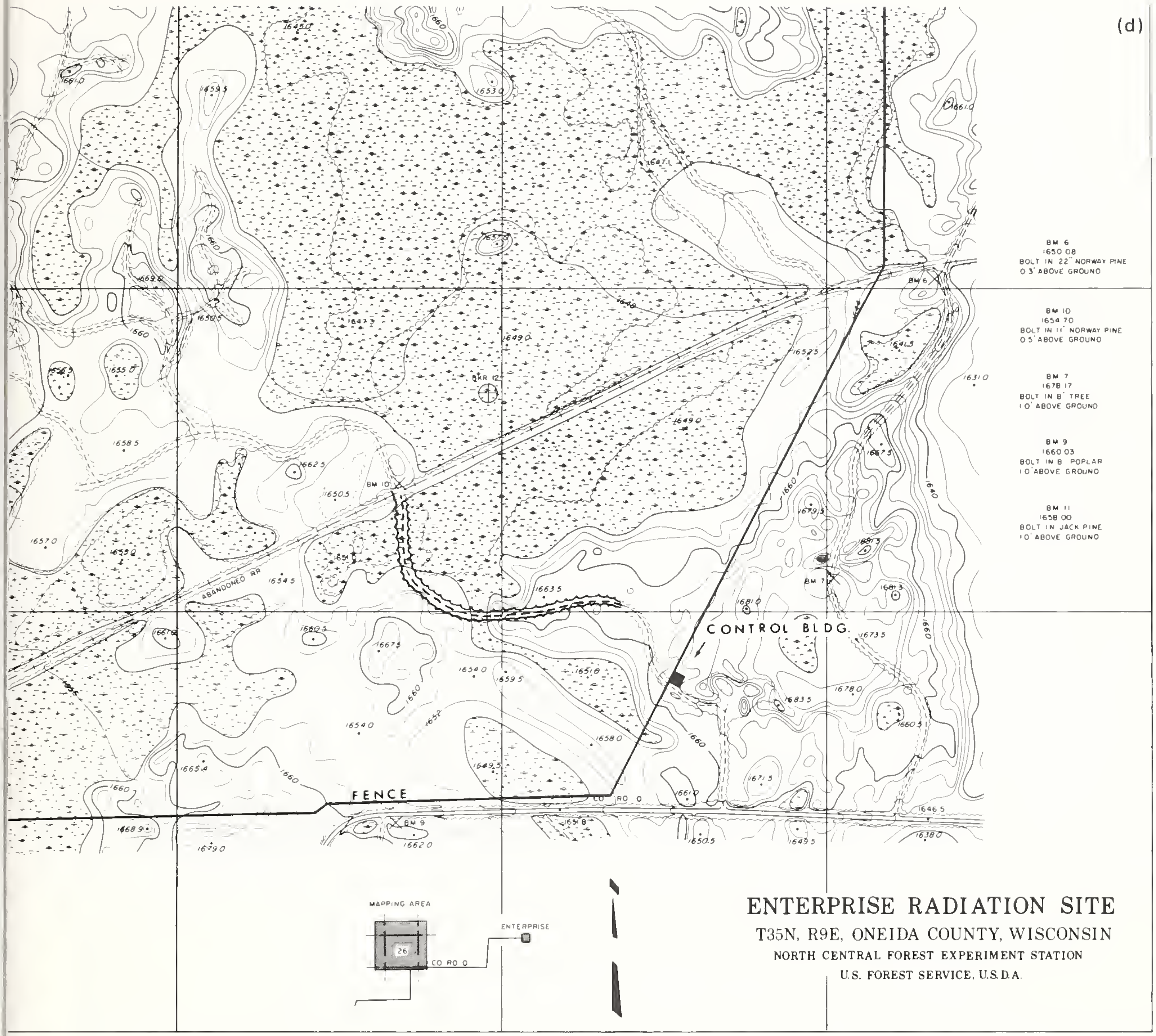


Fig. 3d Enlargement of lower right quadrant of contour map.

Fig. 4 Soil-type map of the Enterprise Radiation Forest. The three numbers within each delineated area of upland soils indicate the soil name, percent slope, and erosion potential, respectively. Erosion symbol 1 indicates little or no erosion (See Table 1).

approximately 150 m (500 ft) from the source. It is weighted with a 5.8-kg (~10-lb) lead brick at the far end to keep it taut and to prevent entanglement. The cable is suspended through pulleys attached to the trees, and a 2.3-kg (~5-lb) weight between two of the suspended pulleys permits the source to be raised and lowered while keeping the trip cable tight.

The radiation source is raised out of the lead shield approximately 5 ft to irradiate the surrounding area and is lowered into the shield to permit workers to enter the area. The radiation source is operated entirely electrically and automatically from the control building, with the exception of the provision for dropping it into the shield with the trip cable described in the event of emergency or mechanism malfunction.

Irradiation of Site 1

Initial operation of the source was on May 3, 1972, and, after some additional modifications to accommodate daily operation, the source was operated on the planned 20 hr/day schedule from 1230 to 0830 until Oct. 16, 1972.

Surveys have shown that the highest radiation levels at the fence at its closest point to site 1 are less than 3 mr/hr.

Table 1

SOILS OF THE ENTERPRISE RADIATION FOREST, AS ILLUSTRATED IN FIG. 4

Code	Soil type	Description
06	Couderay peat	The poorly drained, nearly level Couderay soils formed from the remains of sedge and woody plants occupy basins that were once shallow glacial lakes. A thin surface of sphagnum moss or moss peat covers most areas. These soils are strongly acid and are very low in mineral fertility. The water table is at or near the surface, and ponding of water occurs in most areas. These soils are difficult to drain. Drainage results in shrinkage; after draining, wind erosion and burning are severe hazards. A very short growing season with frequent summer frost severely limits plant variety and growth.
06-L	Couderay peat over loams	This soil is less than 42 in. of organic remains over loamy mineral soil. It is otherwise similar to Couderay peat and has similar problems.
11	Goodman silt loam	The well-drained, gently sloping soils of the Goodman series developed in a silt mantle over acid, sandy loam glacial till and occupy glacial uplands. The upper 30 in. is silt loam. The underlying glacial till ranges from loamy sand to sandy loam and in places contains pockets or lenses of sand. Stones are few to common on the surface and within the soil. These are good soils for the production of forest and wildlife.
18	Monico loam	The somewhat poorly drained, gently sloping soils of the Monico series developed in acid, loamy glacial till and occupy lower slopes and upland drains in glacial uplands. Stoniness ranges from moderately to very stony. Monico soils have a slight erosion hazard and are wet because of seepage and runoff water from higher land.
21	Iron River loam	The well-drained, gently sloping soils of the Iron River series developed in acid, sandy loam glacial till and occupy glacial uplands and moraines. The texture of the upper layers is sandy loam or loam. The underlying glacial till ranges from loamy sand to light loam and in places contains pockets or lenses of sand. Stones ranging to several feet in diameter are few to numerous on the surface and throughout the soil layers. Sloping areas have a water-erosion hazard. These are good soils for the production of forest and wildlife.
104	Padus loam	The well-drained sloping soils of the Padus series developed in loamy glacial drift underlaid by stratified acid sand and gravel and occupy glacial outwash plains and stream terraces. The texture in the upper 18 in. ranges from loam to fine sandy loam. The depth to loose substratum varies from 20 to 40 in. Stoniness varies from slight to moderate. Padus soils on slopes have a water-erosion hazard. They are slightly drouthy.
151	Gaastra silt loam	The somewhat poorly drained, nearly level soils of the Gaastra series developed in silt and fine sand glacial water deposits and occupy glacial lake basins. The texture of the upper 40 in. is silt loam or silt with thin layers of fine sand. These soils occupy low positions and have a high water table and a high available moisture-supplying capacity.

Fig. 5 Control building, entrance gate, and fence.

Fig. 6 The 10,000-Ci ^{137}Cs radiation source in position in site 1.

Dosimetry on site 1 is intensive and is described in Chap. 2 of this volume.

Public Relations

Informing the public about the research on the radiobiology of natural northern forest communities in the Enterprise Forest is a continuous task. Since the project was initiated, we have received and responded to numerous written inquiries from individuals, ranging from interested local citizens to state and national legislators. In addition, several environmental groups requested and were provided information on the research.

Press, radio, and television coverage of the development of the research facilities at Enterprise and of the research progress has been frequent. Especially well covered were the efforts to remove the deer from the forest. A detailed description of the live trapping (described in Chap. 11) was released to all news media in Wisconsin on Feb. 17, 1972. This was followed by a release on Mar. 17, 1972, reporting the success of the live-trapping and also announcing the special permit for hunting and shooting the remaining deer. No significant adverse reactions to the deer removal were encountered.

An environmental impact statement covering all aspects of the radiobiology project has been prepared. In-house review has been completed, and a draft of the statement was made available to the Environmental Protection Agency and to the public for review. The final environmental impact statement was filed in 1974.

ACKNOWLEDGMENT

The generous assistance of Richard R. Buech and Edmund O. Bauer in preparing the illustrative material is greatly appreciated.

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Description of Experimental Plot Design of Site 1 and the Control Area

2

B. J. SALMONSON, R. W. BLANK, and R. L. NELSON
Institute of Forest Genetics, North Central Forest Experiment Station, Forest Service, U. S. Department of Agriculture, Rhinelander, Wisconsin

ABSTRACT

Initial studies in the Enterprise Radiation Forest were begun in 1968, and the locations of radiation site 1 and the control area were selected in July 1969. Once the location of site 1 was determined, work was immediately begun to establish transects and sampling plots in site 1 and the control area. Weather stations established in 1968 have been maintained since that time. During August 1969 the ground vegetation was sampled and the species were identified. Also at that time the trees were numbered, measured for diameter at breast height, and identified. In June 1970 the exact locations of the trees relative to the center of site 1 were determined by transit. Small mammal trapping grids were also established in the spring of 1970, and a systematic live-trapping schedule was initiated. The dosimetry design was formulated in 1971, and the field work was completed early in 1972. A detailed description of the methods used in establishing the experimental-plot design in site 1 and the control area is presented.

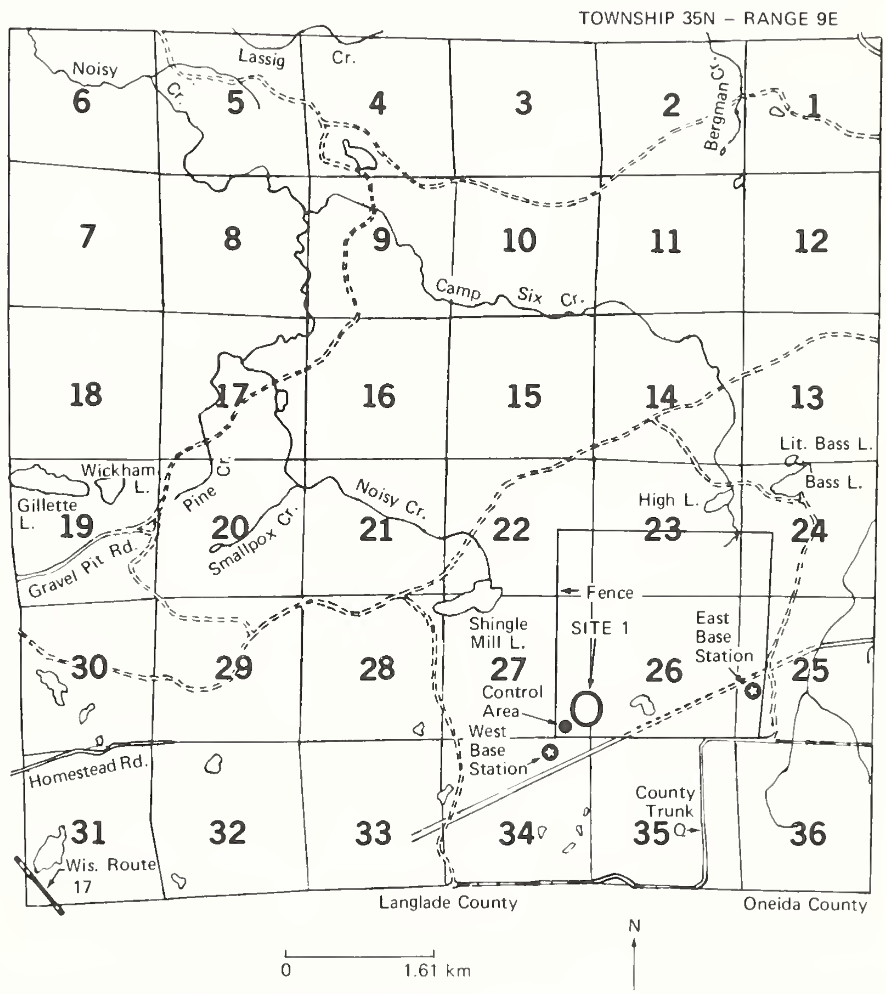


Fig. 1 Township map showing location of the Enterprise Radiation Forest fence, control area, site 1, East Base Station, and West Base Station.

GENERAL DESCRIPTION OF SITE 1 AND THE CONTROL AREA

Location

The Enterprise Radiation Forest, site 1, located in the southwest corner of the 1440-acre Enterprise tract (see Chap. 1, Fig. 1, this volume, for exact location in Wisconsin), was selected as the first experimental area for radiobiological studies of typical northern forest communities (Fig. 1).

Topography

The relief of site 1 and the control area was formed from glacial morainal material and can be classified as gently rolling to hilly, with bogs interspersed within the low-lying areas. The average elevation of site 1 and the control area is approximately 511 m above mean sea level. The 300-m-diameter site 1 area has slopes varying from nearly level to a maximum of 17% (Chap. 1, this volume), with most of the area having a slope of 9% or less. The control area, located approximately 400 m southwest of site 1,

has slopes similar to those found within site 1 except for one rather large hill with a southern exposure where in some instances slopes exceed 17%.

Soils

Soil types within site 1 and the control area are primarily Iron River loams, with Couderay peat in most of the bog areas. In addition, a small portion of the control area is covered by a Monico loam (Chap. 1).

Climate

In general, the climatic conditions can be classified as temperate continental. Summer temperatures, recorded under the forest canopy at 46 cm above the ground during 1971 and 1972, ranged from 34.44°C (94°F) to −2.22°C (28°F); the highest temperature usually occurs in May. Extreme temperature fluctuations also occur in winter; the recorded maximum was 2.78°C (37°F), and the minimum was −40°C (−40°F). The absolute minimum temperature recorded at Enterprise Forest was −46.67°C (−52°F) on Jan. 15, 1972, at the East Base Weather Station, which is located approximately 1.5 miles east of site 1. The average annual rainfall for site 1 and the control area, recorded May through October 1971 and 1972, was 51.69 cm (20.35 in.), and the average maximum snow depth at any one time, recorded during winters of 1970–1971 and 1971–1972, was 78.54 cm (30.92 in.), which occurred on Mar. 22, 1971, and Mar. 8, 1972. (Note: All temperature and precipitation measurements have been converted to the international system of units.) The growing season at Enterprise is approximately 5 to 6 months long, usually beginning in the last week of April and extending to the last week of September; for some species it runs to the end of October. Frosts are known to occur during any month of the year, however.

Flora and Fauna

The plant and animal communities found in site 1 and the control area are characteristic of those found in most second-growth northern forests (see Chaps. 4, 5, 7, 11, and 12, this volume).

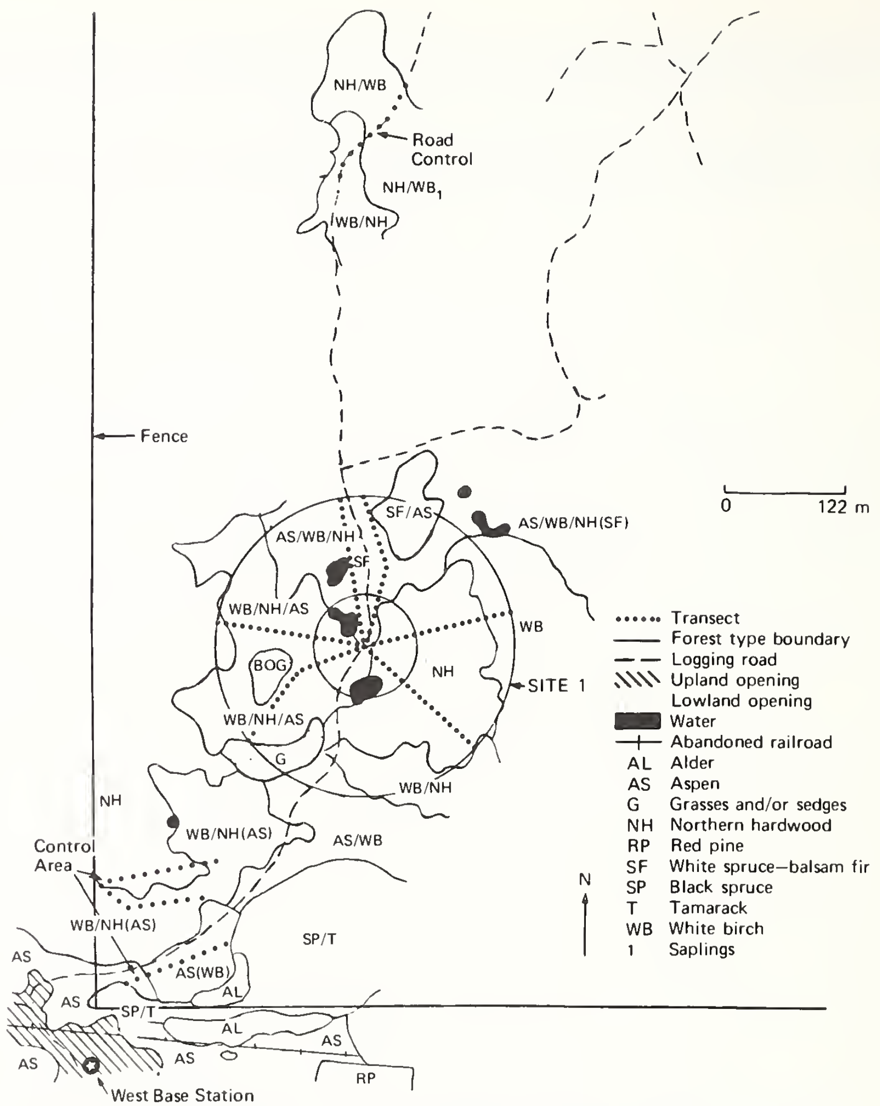


Fig. 2 A portion of the forest-type map showing site 1, West Base Station, and control area (including "road" control).

TRANSECT AND PLOT DESIGN OF SITE 1 AND THE CONTROL AREA

Transects

The experimental plots established along two transects in each of the three forest types (aspen, white birch, and northern hardwood) radiate out from a central point and extend to a distance of 150 m (Figs. 2 and 3). The azimuth defining the location of each transect within a forest type was randomly selected with the stipulation that, if a transect extended beyond a given forest type, another randomization would be made to keep it in the type. Only two of the six transects had to be rerandomized, one each in the aspen and birch forest types (Figs. 2 and 3). An additional transect was established on the abandoned logging road that intersects the experimental area (Fig. 2).

A 100-m transect was laid out at random in each of the three forest types in the control area (Fig. 4). An additional 100-m transect was established as a control on a logging road approximately 0.25 mile north of the present study area (Fig. 2).

Ground-Vegetation Plots

Ground vegetation is defined as all herbaceous species and woody species less than 0.3 m in height (Chap. 6, this volume). For ground-vegetation measurements contiguous paired 0.5- by 0.5-m sample plots were established between 5 and 10 m from the radiation source along

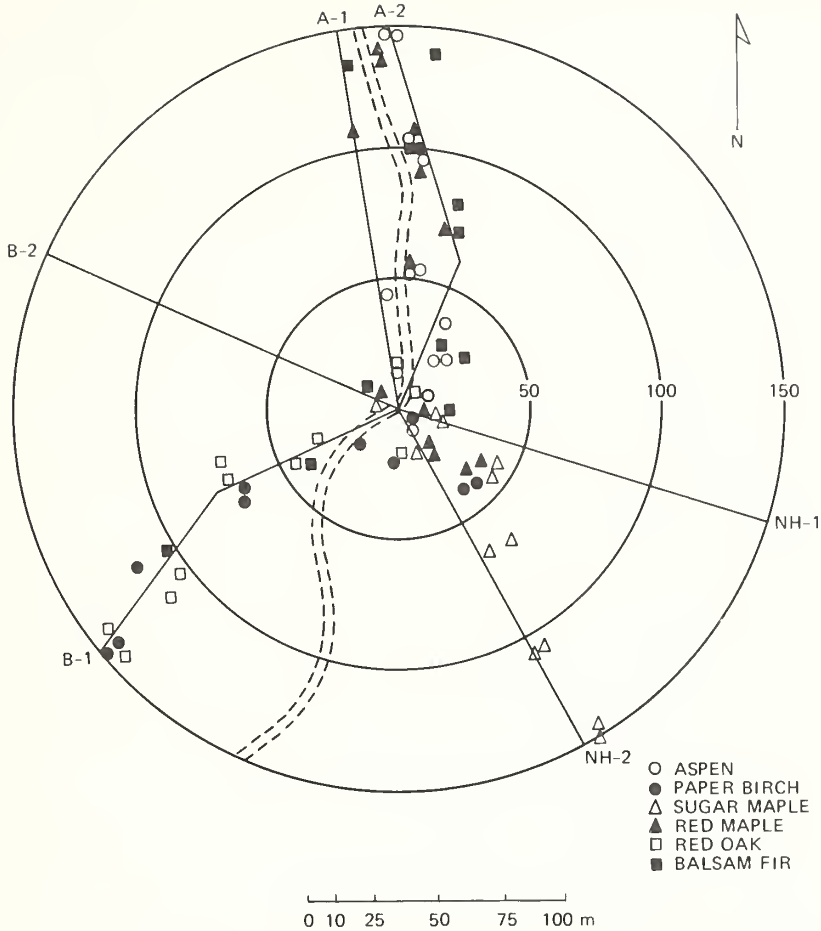


Fig. 3 Site 1 transect layout and location of trees selected for phenological studies. Transects are A-1 and A-2, aspen; B-1 and B-2, birch; and NH-1 and NH-2, northern hardwood.

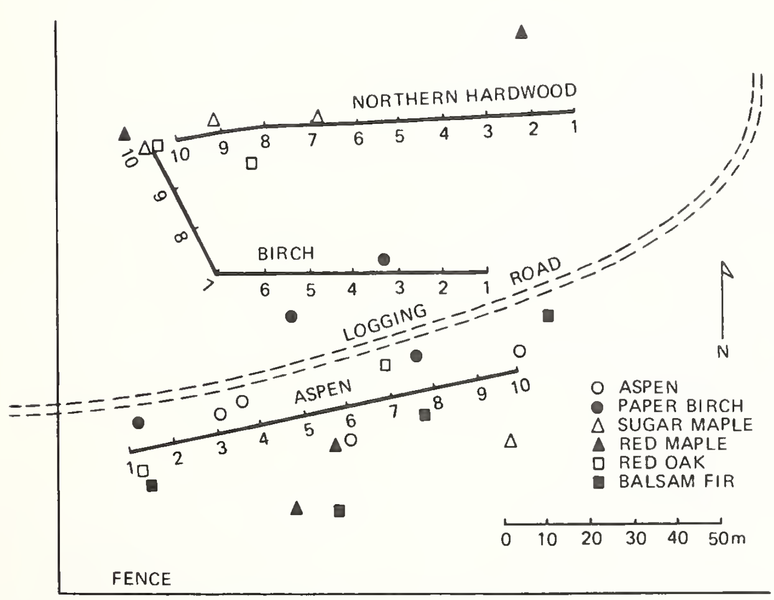


Fig. 4 Location of sample transects and trees selected for phenological studies in control area. Plots for sampling ground vegetation were established at each of the numbered points along the lines.

each of the seven experimental transects, and paired 1- by 1-m plots were located at the following distances from the source: 10, 12, 14, 16, 18, 20, 25, 30, 35, 40, 45, 50, 60, 70, 80, 90, 100, 110, 120, 130, 140, and 150 m (Fig. 5). A detailed layout of the sample plots is presented in Chap. 6, Table 1.

Tubular aluminum stakes were set up on each transect at each of these distances, and the corners of the plots were marked with flagged wire stakes. To protect the plots from accidental trampling, we placed wooden stakes off the corners and strung twine around the perimeter (Fig. 6).

Along each control transect aluminum stakes placed at 10-m intervals were numbered from 1 to 10 (Fig. 4). At each of these points, paired 1- by 1-m plots were established for sampling ground vegetation. For the logging-road control transect, paired 1- by 1-m plots were located at 10-m intervals for a total of 20 plots. Corners of each plot were marked, and sample plots were protected from trampling in the same manner as in site 1.

Shrub Sample Plots

Paired 2- by 1-m plots for sampling low shrubs (0.3 to 1.0 m high) and paired 2- by 2-m plots for sampling tall shrubs [greater than 1.0 m high and less than 2.5 cm in diameter at breast height (dbh)] were established at 5-m intervals between 5 and 50 m and at 10-m intervals between 50 and 150 m from the radiation source. A total of 40 plots of each size were located along each of the six transects in site 1 (Fig. 7). There were no shrubs on the logging-road transect. In the control area paired plots of the same size were used for sampling low and tall shrubs at the 10 points on each of the three transects. The identification system for individual plots used for ground-vegetation and shrub sampling is shown in Figs. 8 and 9.

METHODS OF SELECTING TREES FOR PHENOLOGICAL STUDIES

Phenology Trees

The selection of six tree species for phenological studies was based upon availability, dominance, the visibility of their upper crown portions for photo-

graphic purposes, and proximity to weather stations, soil pits, and litter traps. In site 1 a total of 70 trees was selected for study; where possible, these included two individuals of each species at 10, 20, 40, 70, 110, and 150 m (Fig. 3). Phenological observations were also carried out on 19 additional trees of two other species occurring at scattered points in site 1. In the control area, four individuals of each species were selected primarily on the basis of visibility of the upper crown (Fig. 4).

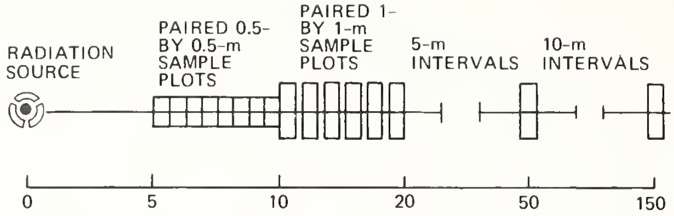


Fig. 5 Layout of sample plots on site 1 for ground-vegetation sampling.

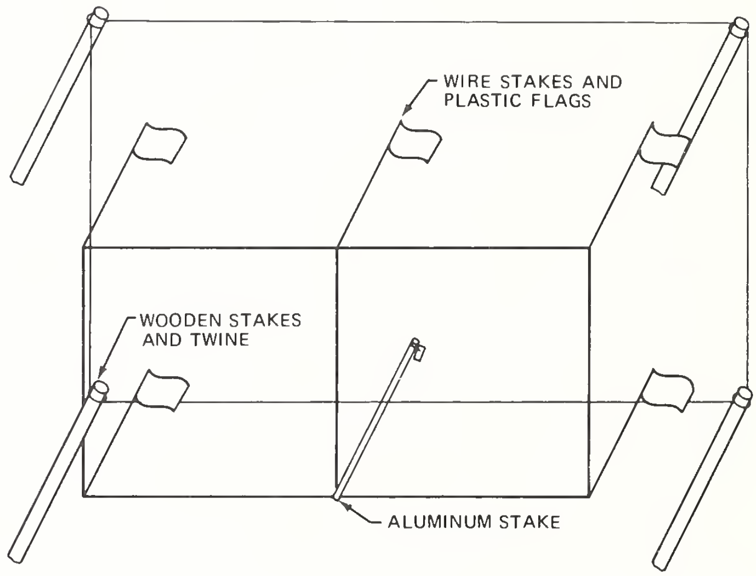


Fig. 6 Marking and protection by twine of plots used for ground-vegetation sampling.

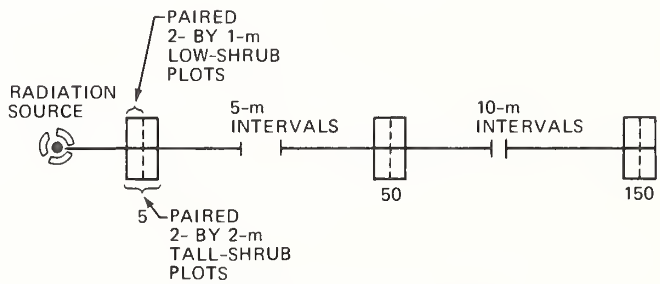


Fig. 7 Layout of plots on site 1 for sampling shrubs. Paired plots of two sizes, 2 by 1 and 2 by 2 m, were nested for sampling low and tall shrubs, respectively.

Other Tree Locations and Measurements

In site 1 all trees with a dbh of 2.5 cm or larger and within 50 m of the site center were numbered. We followed the North Central Forest Survey Field Instruction Manual (Essex, Ostrom, and Stone, 1967) to obtain tree measurements, such as dbh and heights. Tree heights were measured from the ground with a Haga hypsometer or directly with a height pole. Horizontal distance and elevation of each tree in relation to the source location were calculated from transit data.

A map showing species, location, and size of each tree within 50 m from the site center and a topographic map were prepared (Figs. 10 and 11). Between 50 and 150 m from the center of site 1 and in the control area, trees within 10 m of each transect were numbered, plotted on a grid, and measured as described.

WEATHER AND RECORDING STATION MEASUREMENTS

Base Station

A weather and microclimate base station, called the West Base Station (Figs. 1 and 2), was established in a 2-acre grassy clearing near the southwest corner of the Enterprise Forest and was operated from June 1968 to December 1970. The base station was located in an open environment so that data recorded would come from a site comparable to U. S. Weather Bureau recording stations. From studies conducted by Ringger (1972) and as dictated by the height of the trees surrounding the base-station site, it was determined that the minimum forest opening required to simulate a microclimate comparable to that of a totally open area would be approximately 2 acres in size. The ratio between the diameter of the opening and the height of the surrounding trees must be greater than 2 : 1.

When the security fence was erected around the perimeter of the 1440-acre tract during the winter of 1970–1971, the West Base Station was discontinued. A new station (also about 2 acres in size), known as the East Base Station, was established within the fenced area about 1.5-miles east of the first station (Fig. 1). This station began operating in September 1970 and is the main weather station for continuing studies.

The following instruments are employed at the East Base Station: (1) one

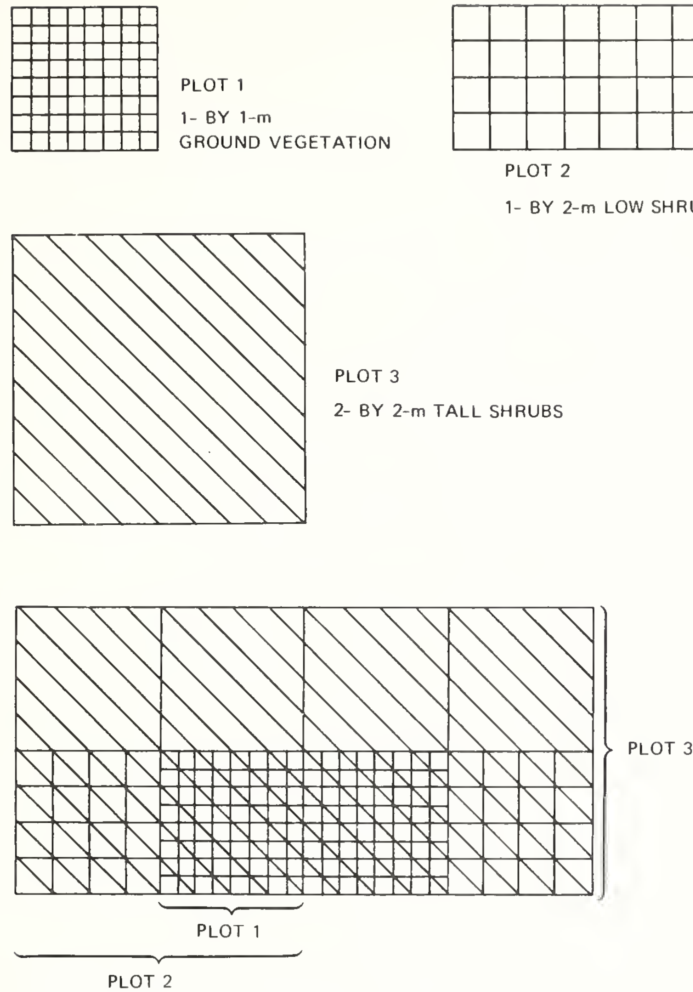


Fig. 8 Size and nesting of plots used for sampling ground vegetation and shrubs.

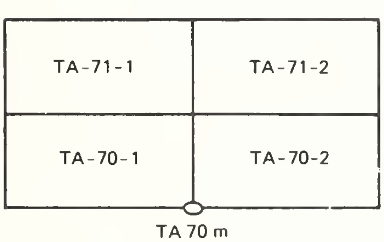


Fig. 9 Identification of plots used for shrub sampling. TA, name of transect; 70 and 71, distance from radiation source, in meters; 1 and 2, plot on left or right side, respectively, when proceeding away from the source.

standard 8-in. rain gauge, (2) three snow-measurement sticks, (3) one remote-recording propane-heated snow gauge, (4) one direct-reading cup anemometer (5) one mechanical pyranograph, (6) three hygrothermographs, (7) one maximum thermometer, and (8) one minimum thermometer (Fig. 12).

Recording Stations in Site 1 and the Control Area

A recording station is a location where data are collected (the types of data collected are described here). Eighteen recording stations were established in site 1 and the control area. The stations were located at 10, 20, 40, 70, 110, and 150 m from the radiation source along three of the six experimental transects (aspen, A-2; birch, B-1; and northern hardwood, NH-2) (Fig. 3) and at points 3, 5, and 7 (20, 40, 60 m, respectively) along each transect in the control area (Fig. 4). In site 1 the starting point for locating the recording stations along the transects was based on predicted radiosensitivities of the plant species within the area (Chap. 13, this volume), and the remaining locations were determined from mathematically predictable radiation levels that follow the inverse-square law. In the control area the initial point was established at random, and the remaining points were established systematically.

Each recording station had the following instruments and equipment (Figs. 13 and 14):

(1) Two 0.25-m^2 combination seed and litter traps and two traps for light airborne seed. Each combination seed and litter trap consists of two trays, an upper tray with a bottom of 6-mm mesh hardware cloth and a lower tray of 1-mm window screening (Fig. 15). Because it was believed that aspen seed would blow out of the seed and litter traps, two 0.25-m^2 traps 76 cm deep with sides of 1-mm mesh window screen and a double layer of cheese cloth attached to the bottom were also placed at each station. In the control area, only one litter trap and one aspen seed trap at each location were used.

(2) Two vials filled with petroleum-ether chlorophyll extract for measuring solar radiation attached to plot location stakes at each station and also at 15, 25, 35, and 50 m. In the control area the vials were located at points 1, 3, 5, 7, and 9.

(3) One Van Arsdel weather shelter (Van Arsdel, 1963) with a maximum and/or minimum thermometer, a mercury thermometer, and a 7-day hygrothermograph.

(4) One standard 8-in. rain gauge and one snow-measurement stick.

(5) Three Soiltest standard soil-moisture cells (model MC-310A) for measuring soil moisture and temperature at depths of 7.5, 20, and 50 cm (Fig. 16). Each soil-moisture cell contains a small thermistor for measuring the temperature of the surrounding medium.

Composite soil samples for future microbiological and chemical analyses were taken along transects A-2, B-1, and NH-2 at distances of 5, 7, 10, 15, 20, 25, 40, 50, 70, 110, and 150 m from the source location and in the control area at points 1, 3, 5, 7, and 9 along all three transects. Twenty soil cores were taken at each location, ten on either side of the transect. The soil cores were taken to a depth of 30 cm and were divided into three sections, 0 to 7.5, 7.5 to 15, and 15 to 30 cm. One-third of each sample was frozen and stored for microbiological study, and the remainder was oven-dried and retained for chemical analyses.

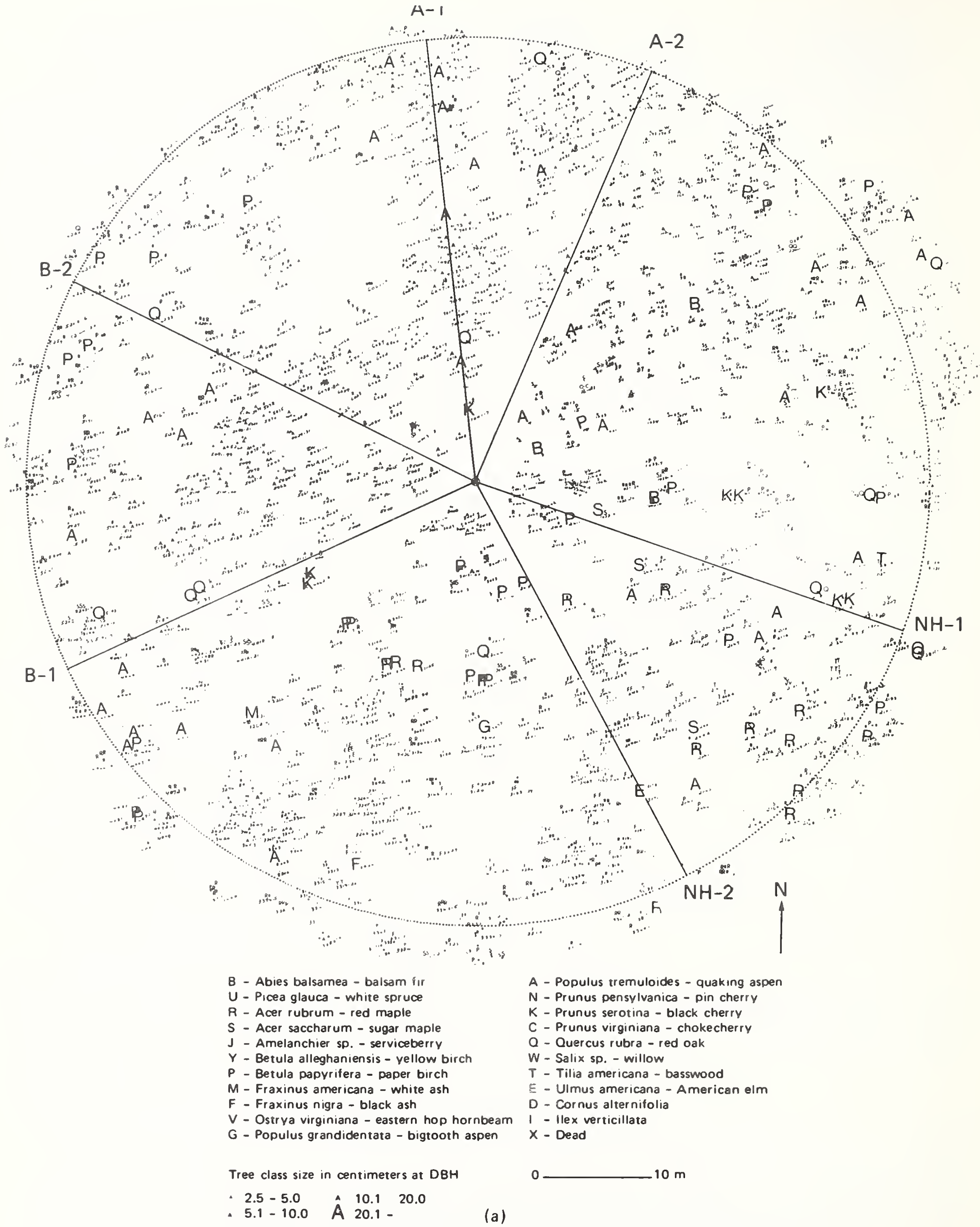
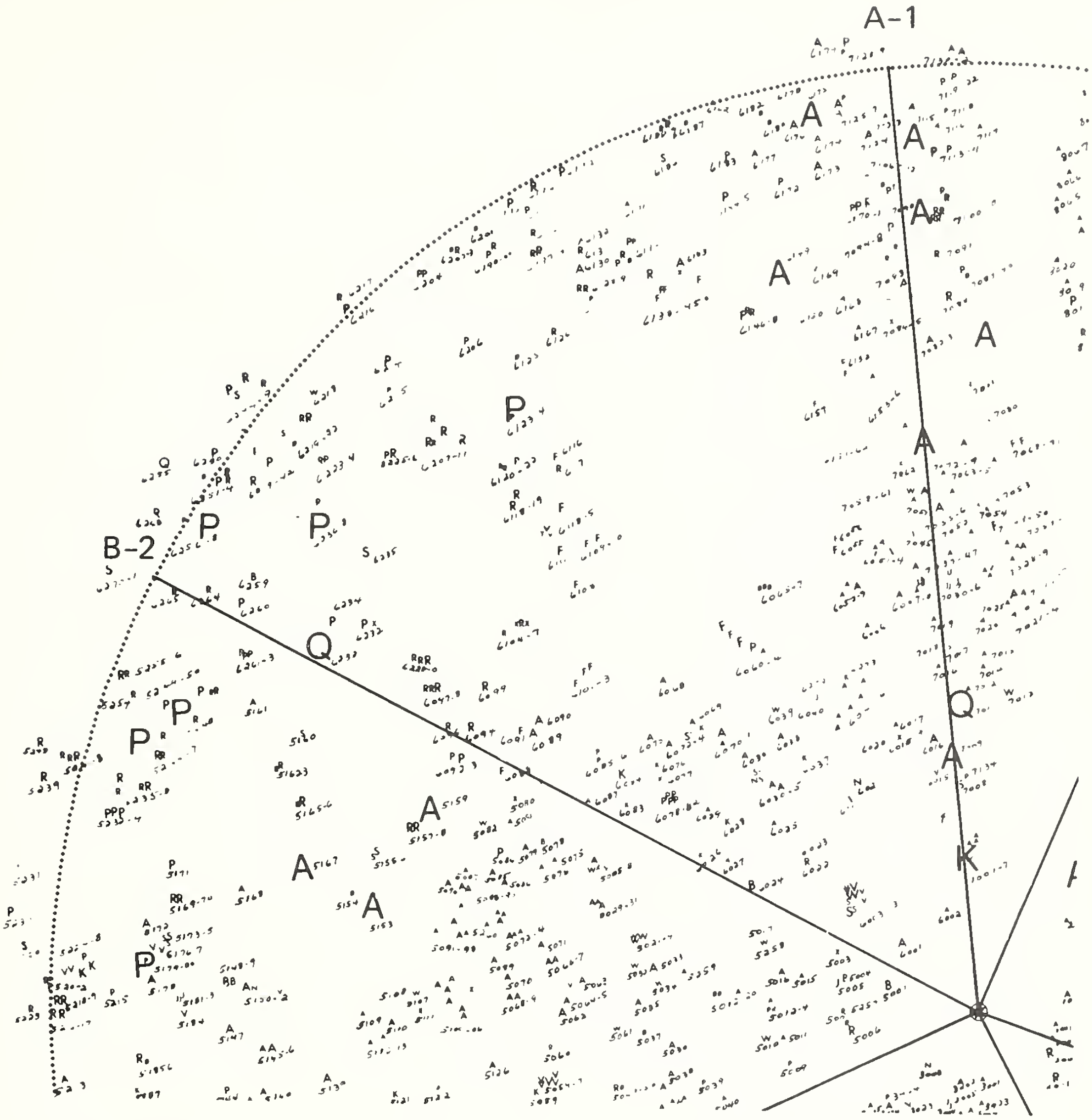


Fig. 10 Site 1 map of all trees within 50 m of the radiation source by size and species (trees with a dbh less than 2.5 cm are not shown). (a) Entire map. (b to e) Enlarged views of map sections.



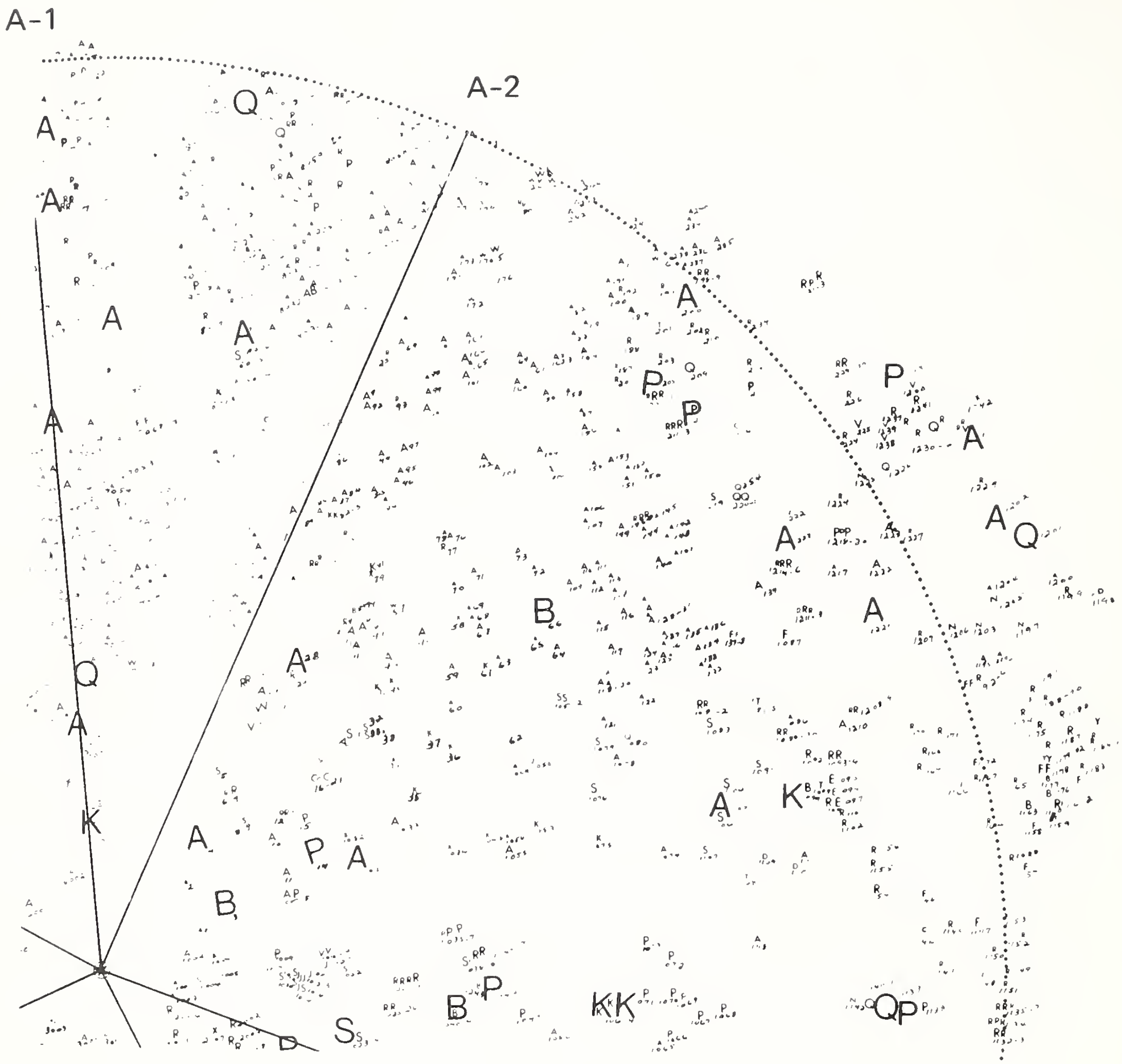
B - Abies balsamea - balsam fir
U - Picea glauca - white spruce
R - Acer rubrum - red maple
S - Acer saccharum - sugar maple
J - Amelanchier sp. - serviceberry
Y - Betula alleghaniensis - yellow birch
P - Betula papyrifera - paper birch
M - Fraxinus americana - white ash
F - Fraxinus nigra - black ash
V - Ostrya virginiana - eastern hop hornbeam
G - Populus grandidentata - bigtooth aspen
A - Populus tremuloides - quaking aspen
N - Prunus pensylvanica - pin cherry
K - Prunus serotina - black cherry
C - Prunus virginiana - chokecherry
Q - Quercus rubra - red oak
W - Salix sp. - willow
T - Tilia americana - basswood
E - Ulmus americana - American elm
D - Cornus alternifolia
I - Ilex verticillata
X - Dead

Tree class size in centimeters at DBH

ᐧ 2.5 - 5.0
ᐞ 5.1 - 10.0
ᐃ 10.1 - 20.0
A 20.1 -

0 —— 10 m

(b)



B - Abies balsamea - balsam fir
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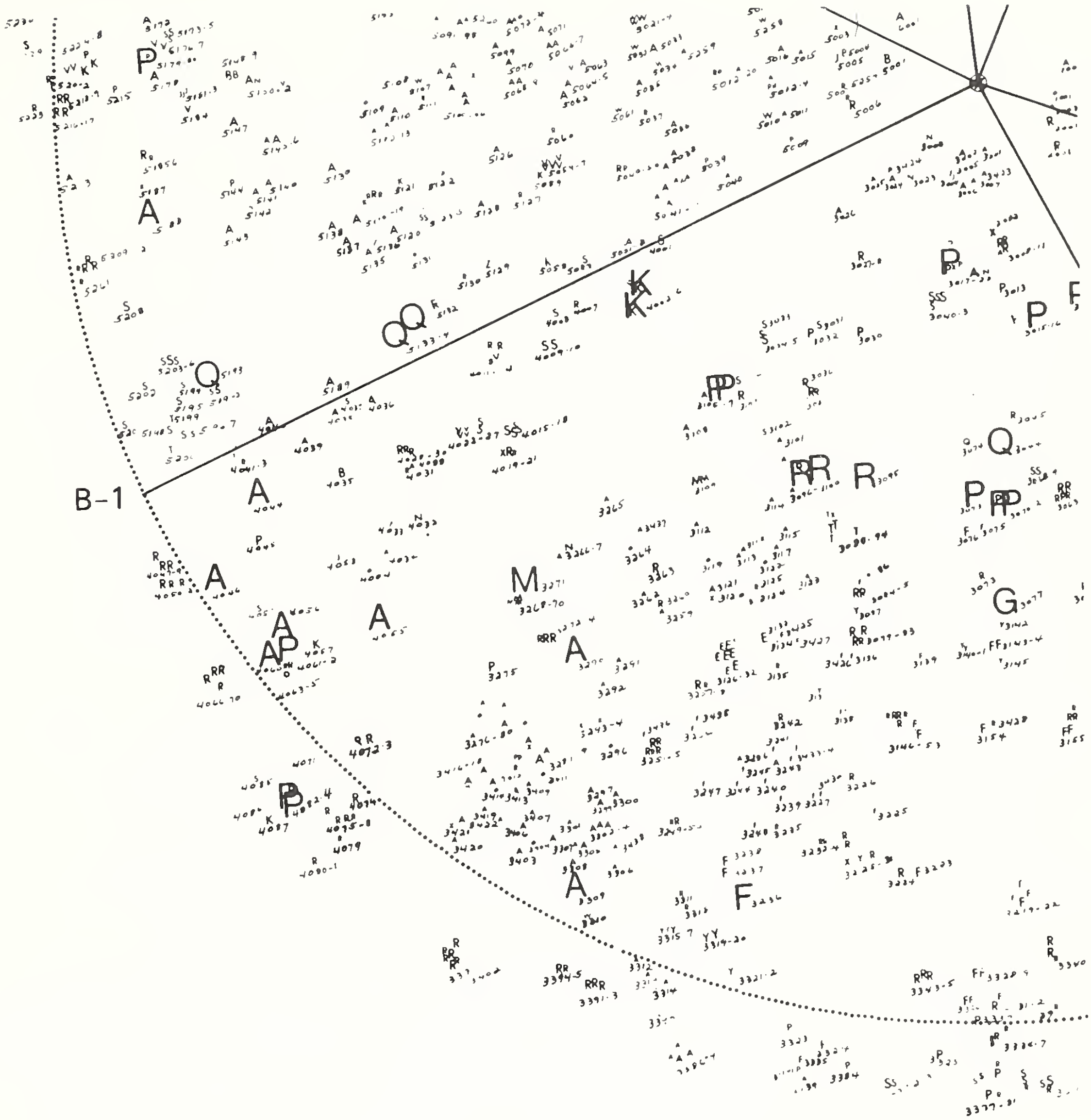
D - Cornus alternifolia
I - Ilex verticillata
X - Dead

Tree class size in centimeters at DBH

· 2.5 - 5.0
▴ 5.1 - 10.0
▲ 10.1 - 20.0
A 20.1 -

0 ——— 10 m

(c)



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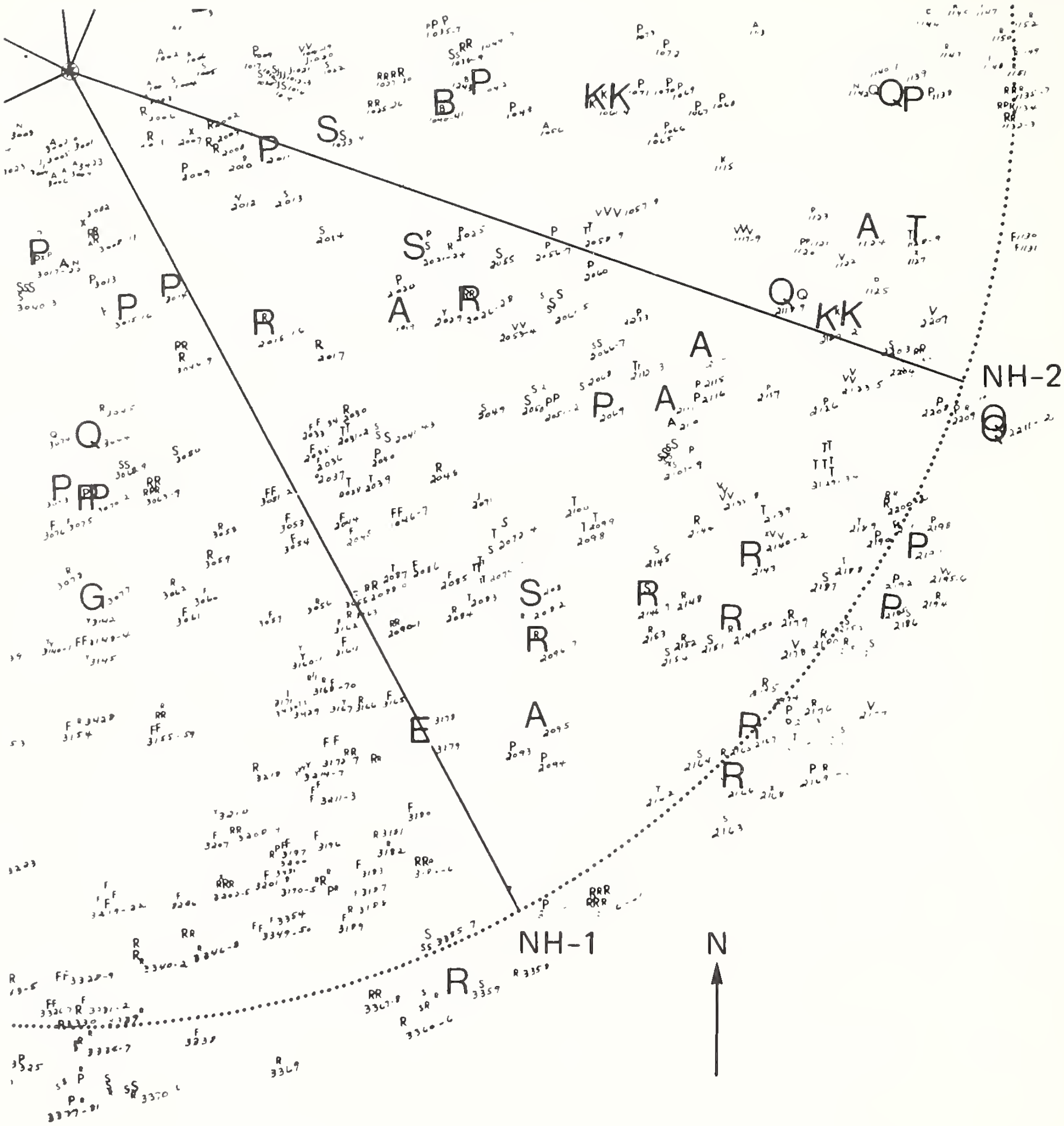
W - Salix sp. - willow
T - Tilia americana - basswood
E - Ulmus americana - American elm
D - Cornus alternifolia
I - Ilex verticillata
X - Dead

Tree class size in centimeters at DBH

· 2.5 - 5.0
▴ 10.1 - 20.0
. 5.1 - 10.0
A 20.1 -

0 ———— 10 m

(d)



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I - Ilex verticillata
X - Dead

Tree class size in centimeters at DBH

0 ———— 10 m

· 2.5 - 5.0
▴ 5.1 - 10.0
▴ 10.1 - 20.0
A 20.1 -

(e)

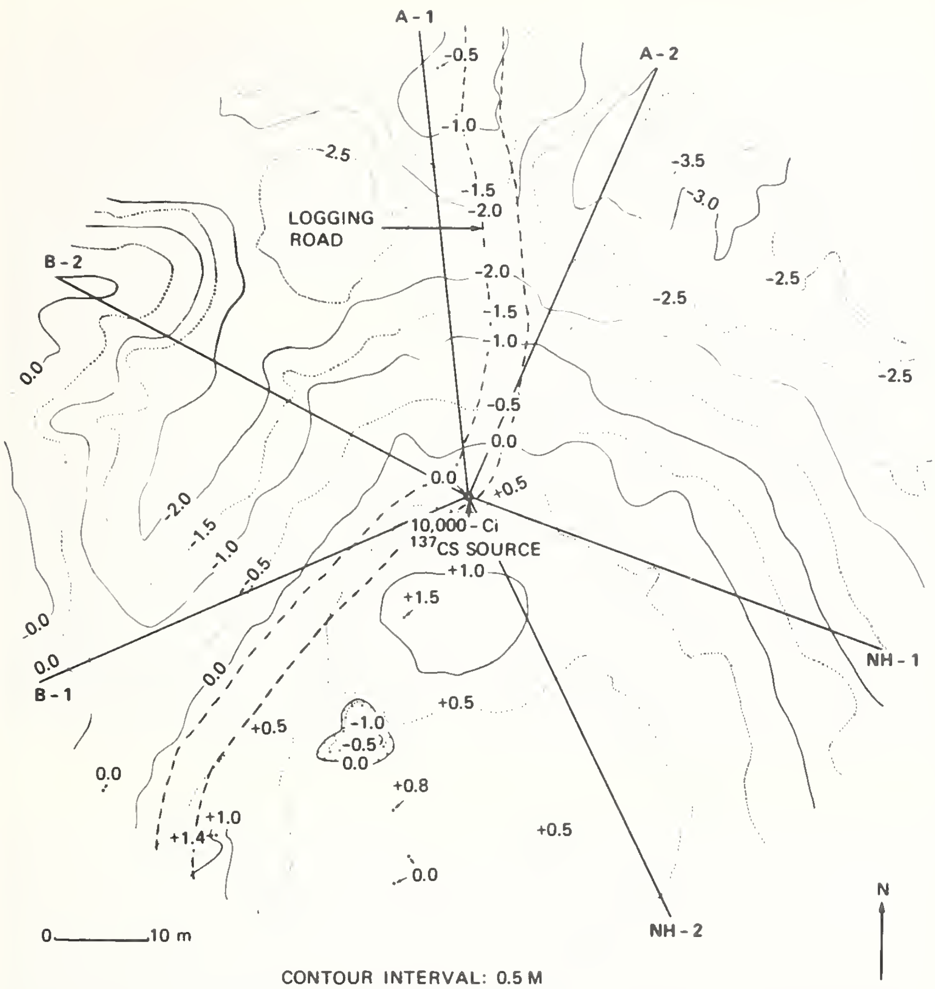

Fig. 11 Contour map of the area within 50 m of source location in site 1. Vertical data are relative to zero ground level at the base of the radiation source.

Fig. 12 Weather instruments and equipment located at the East Base Station.

SMALL-MAMMAL TRAPPING GRIDS

To study the impact of radiation on wild small-mammal populations, we began a systematic trap–retrap study at Enterprise in the spring of 1970. Circular live-trap grids were laid out in site 1 (Fig. 17) and in the control area (Fig. 18). Methods of trapping and location of grids are described here.

In site 1 the location of the radiation source was used as the center of a circular grid. Through this point an east–west base line extending 135 m from the center in both directions was established. North–south transit lines were run from the base line at 15-m intervals. Stakes were placed at 15-m intervals along these lines with the restriction that no point would be established at a distance greater than 135 m from the center. The result was a circular grid with a 15-m station interval oriented in the cardinal directions and encompassing 6.2 ha and 277 line-intersect points. Each point was identified by letter and number assigned to the two lines that intersect at its position. Letters designate location with respect to north–south lines, and numbers designate location with respect to east–west lines (see Figs. 17 and 18).

A modified shelter (Iverson and Turner, 1969) was placed at each of the 277 trapping points. The letter–number symbol identifying its location (e.g., A10, J19, etc.) was painted on the lid of each shelter. To help locate the shelter during the winter months under snow cover, we attached a 30-in. wire stake with a flag on top to the northwest corner of the shelter. A small-mammal trap (Buech,

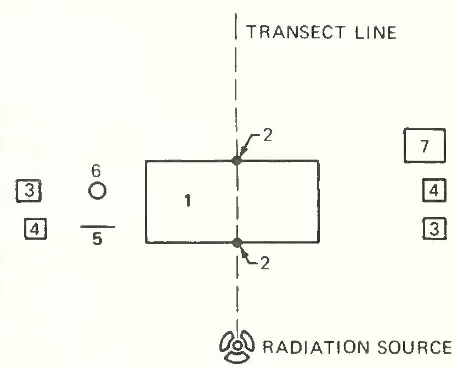

Fig. 13 Typical layout of a recording station. (1) 1- by 2-m sample plots for ground vegetation and shrubs. (2) Aluminum stakes holding chlorophyll vials. (3) Litter traps. (4) Seed traps. (5) Soil-moisture and temperature terminals. (6) Rain gauge. (7) Weather shelter.

1973) baited with peanut butter, rolled oats, and an apple slice was placed at every fourth station. At grid stations within 42 m of the source location, one to four concrete blocks (4 by 8 by 16 in.) were placed next to the shelter to attenuate the radiation exposure to an animal detained in the trap to a computed level of 2 r/hr or less (Fig. 19).

Trapping was conducted for one week in each month. Traps were baited and set on Monday and checked daily until Friday, when the bait was removed and the traps were locked shut. Tuesday through Friday traps were advanced one grid station each day. This scheme provided for a system of partial editing against errors in trap placement or in recording the location of capture because each day of the week had its own set of shelter locations.

The control-area grid is located approximately 400 m southwest of site 1 (Fig. 18). The same type of circular grid was laid out in the control area as in site 1. This grid differs from that of site 1 in that it is only 90 m in radius and covers 2.7 ha and 121 trapping points. The control area was trapped at the same time as site 1.

Fig. 14 Instruments and equipment located at each recording station.

Fig. 15 Combination litter–seed trap with upper tray raised to expose a lower seed-collection tray.

DOSIMETRY DESIGN IN SITE 1

A dosimetry plan was developed for site 1 to give maximum information on radiation exposure received at existing ground-study plots and trees on which detailed phenology measurements are being made.

Ground-Plot Dosimetry

Lithium fluoride (LiF) dosimeters in the form of reusable teflon disks will be placed at three heights (0.0, 0.3, and 1.0 m) on bamboo stakes at each monitored site (i.e., ground-study plot). The site locations for the dosimeters are at the following distances from the source in each of the seven transects: 5.5, 7.5, 9.5, 12.5, 16.5, 20.5, 25.5, 30.5, 35.5, 40.5, 45.5, 50.5, 60.5, 70.5, 90.5, 110.5, 130.5, and 150.5 m. Each week two of these transects will be sampled completely and the other five sampled partially (i.e., thermoluminescent dosimeters will be placed at distances of 5.5, 9.5, 20.5, 30.5, 40.5, 50.5, 60.5, 70.5, 90.5, 110.5, 130.5, and 150.5 m). Each week the transects to be completely sampled will be changed so that every three weeks complete coverage of site 1 is obtained. A total of 346 dosimeters will be used per week for the ground-plot dosimetry.

Within 20 m of the source, dosimeters will be placed underground at a depth of 10 cm at distances of 2, 3, 4, 5, 6, 7, 8, 9, 10, 12, 15, and 20 m. The dose-rate

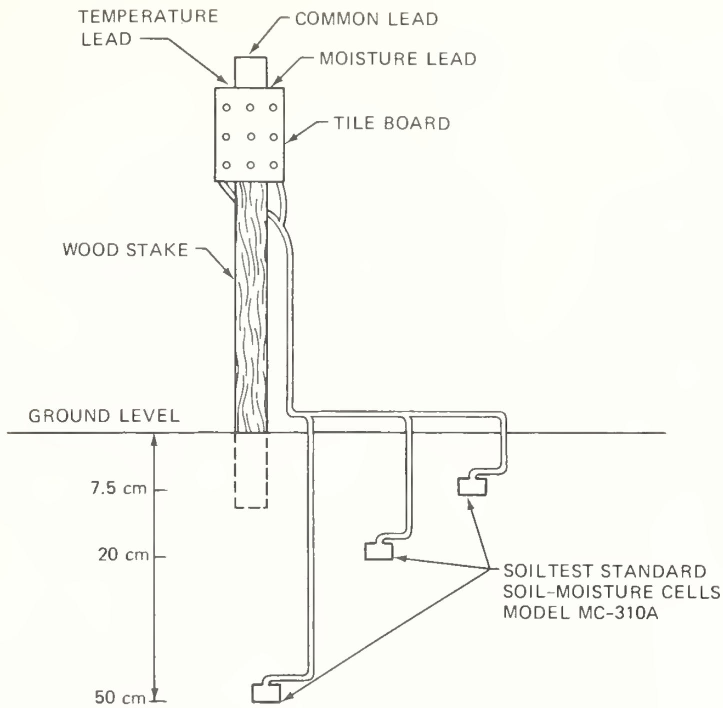

Fig. 16 Diagram showing placement of soil-moisture and temperature cells.

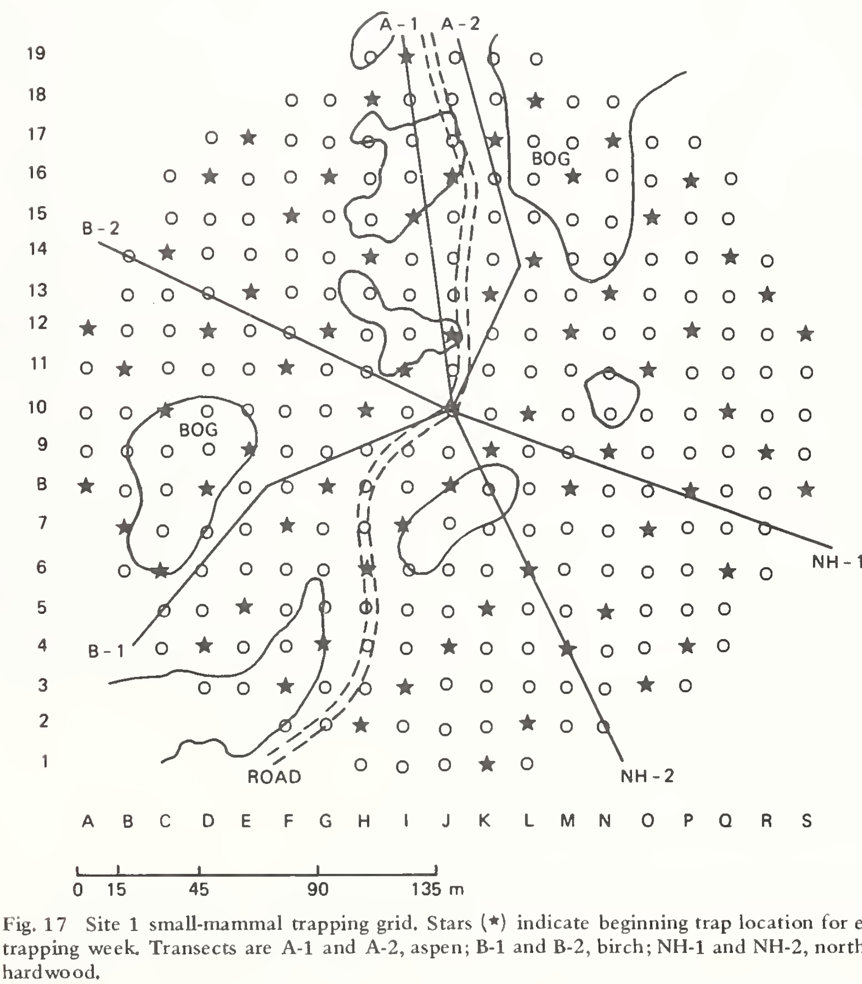

Fig. 17 Site 1 small-mammal trapping grid. Stars (*) indicate beginning trap location for each trapping week. Transects are A-1 and A-2, aspen; B-1 and B-2, birch; NH-1 and NH-2, northern hardwood.

information obtained will be used to determine the radiation exposure received by soil microorganisms and root systems proximal to the source.

Tree Dosimetry

In addition to the ground-plot dosimetry, 101 trees will be sampled in site 1, 89 phenology trees and 12 additional trees selected to provide sufficient points to prepare an isodose map of site 1. Twenty-five of the 101 trees will be included in the weekly dosimeter exchange program. Six dosimeters will be placed in each tree, one on each side of the tree (i.e., on the side facing and the side opposite the radiation source) at heights of 1.5 m and two on each side in the tree crowns, usually at 10 m. Approximately 150 dosimeters will be processed each week for tree dosimetry.

This weekly dosimeter exchange will permit us to detect changes in radiation patterns which may occur with seasonal growth of the vegetation and/or dieback due to radiation damage.

On all 101 trees in site 1 which are used for detailed phenological and other studies, total exposure will be measured using LiF powder in polyethylene capsules that will be left on the trees for the duration of the irradiation period. The total accumulated exposure will be measured at −0.1, 0.0, 1.5, 3.0, 6.0, and 10 m height intervals on both the front and rear of each tree. Approximately 1020 LiF capsules will be used for this purpose. (See Fig. 20 for tree and ground-plot dosimetry stations.)

A daily check on exposures at various distances from the source will be made using Victoreen ionization chambers.

Small-Mammal Dosimetry

Small-mammal dosimetry will also be included in the dosimetry exchange program. During the one week each month when the small-mammal population is livetrapped, small teflon LiF dosimeters will be attached to each individual animal's ear. When the animal is recaptured, the dosimeters will be removed and read.

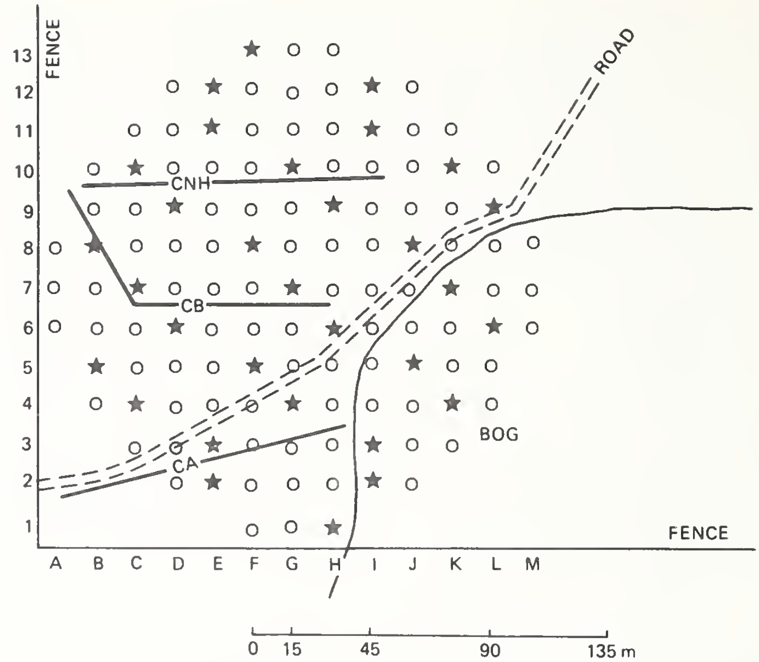

Fig. 18 Control-area small-mammal trapping grid. Stars (*) indicate beginning trap location for each trapping week. Abbreviations are CNH, control northern hardwood; CB, control birch; and CA, control aspen.

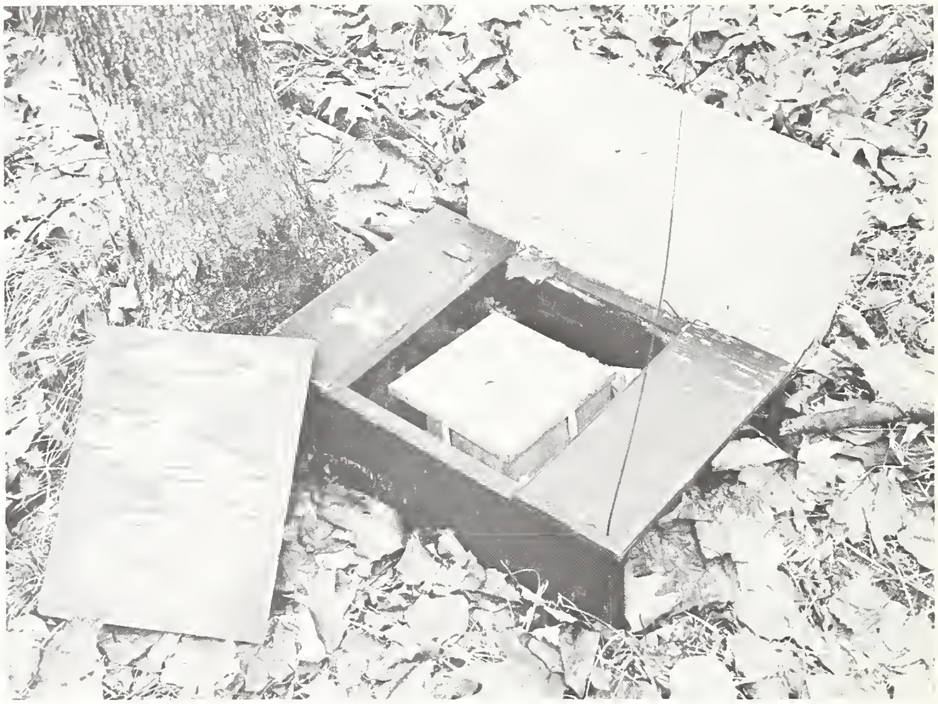

Fig. 19 Trap shelter with concrete blocks for attenuating radiation.

ACKNOWLEDGMENT

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DISCLAIMER

The use of trade, firm, or corporation names in this chapter is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the U. S. Department of Agriculture of any product or service to the exclusion of others that may be suitable.

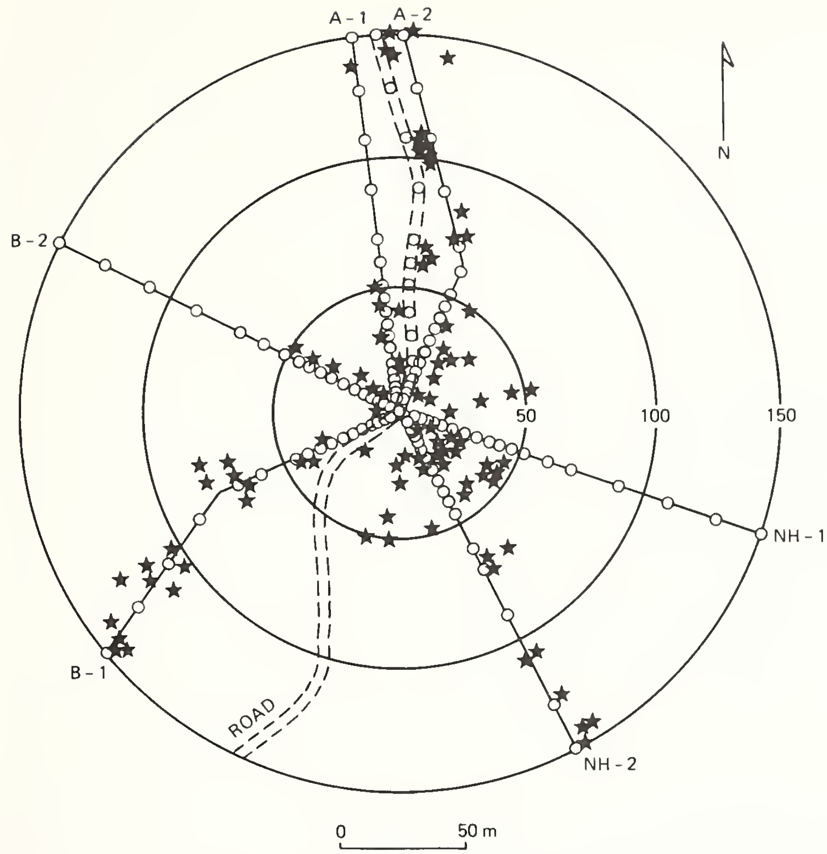

Fig. 20 Diagram of site 1 showing locations of dosimetry stations. Stars (*) indicate tree dosimetry stations, and points (○) indicate ground-plot dosimetry stations.

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Solar Radiation Measurements in the Enterprise Radiation Forest

3

J. ZAVITKOVSKI
Institute of Forest Genetics, North Central Forest Experiment Station, Forest Service, U. S. Department of Agriculture, Rhinelander, Wisconsin

ABSTRACT

Solar radiation was measured in the open and under canopies of several forest types in northern Wisconsin by means of a recording pyranograph and petroleum-ether chlorophyll extracts. Cumulative solar energy in the open was substantially higher in the generally sunny period from April to November 1970 than in the same period in 1971 and 1972, which in both years was cloudy. Depending on cloudiness, the average daily maxima may occur in May (471 langleys in 1972), June (441 langleys in 1971), or July (577 langleys in 1970). Compared with published averages for the Midwest, the measured solar energies were low, probably because of the excessive cloudiness in the Great Lakes region. The highest solar energies under canopies were determined in the aspen forest, followed in decreasing order by birch, maple–aspen–birch, and northern hardwood forest types. Highest absolute solar energies, about 2800 to 3000 langleys/month (or about 20 to 23% of the energy in the open), were determined in all four forest types in May, but relatively more energy (27 to 36%) reached the forest floor in November under leafless canopies. Very low relative values of 2.1, 3.2, 4.2, and 5.9% of the energy in the open were measured under canopies in leaf in the northern hardwood, maple–aspen–birch, birch, and aspen forest types, respectively. Positive and significant correlations were determined between cumulative values measured under canopies at 48 stations in 1970 and 1971. Instantaneous light measurements were positively correlated with the cumulative values, but, for the same number of measurements, instantaneous values were more variable and depending on weather and canopy conditions under- or overestimated the cumulative values. Negative, nonsignificant correlations were determined between basal area or tree density and cumulative solar energy under canopies.

The main objective of this study was to quantify the preirradiation light conditions under canopies of several forest communities and in the open at the Enterprise Radiation Forest in northern Wisconsin. These pretreatment results will be compared with similar observations made during and after gamma irradiation of these communities. The results are also of general ecological and silvicultural interest because available light, more than any other environmental factor, determines successional trends in most forest communities.

The incident light under canopies has been measured in a variety of forest types by foresters, ecologists, and climatologists. An excellent review on this subject is presented by Reifsnyder and Lull (1965). Citing a number of studies from various parts of the world, they say that both intensity and quality of light are modified by closed forest canopies. Canopies of some broadleaf communities reduce light by as much as 99% and even leafless canopies may reduce it by more than 50%. This, they concluded, is by far the highest canopy-caused reduction among the climatic factors such as rainfall (15 to 30%), wind velocity (20 to 60%), or air temperature, which in the summer can be 5°C lower under canopies than in the open.

Light quality within the stand changes with decreasing light intensity. Relatively more solar radiation is transmitted in wavelengths above 700 nm than within the visible spectrum, where only 3 to 14% is transmitted. Light under canopies of broadleaf species is very rich in red and infrared wavelengths in comparison with coniferous stands, where the enrichment in red wavelengths is small (Reifsnyder and Lull, 1965).

Measurements of light in the forest pose complicated problems in environmental research because light varies widely in time and space. Frequently instantaneous light measurements taken under forest canopies are compared to the light in the open. This approach has been criticized because light in the forest in relation to that in the open changes during the day (Minckler, 1961) and because sun flecks, which contribute a large portion of the incident energy, are usually avoided (Eber, 1971). Some of these problems have been eliminated by using integrating devices for solar radiation measurements (Minckler, 1961; Marquis and Yelenosky, 1962; Reifsnyder and Lull, 1965; Perry, Seibers, and Blanchard, 1969; Eber, 1971; and Drew, 1972). In forests where many locations must be monitored, inexpensive chemical light-integrating sensors such as chlorophyll extracts (Perry et al.) provide a useful and effective tool.

METHODS

Incident solar radiation was measured with petroleum-ether extracts of spinach chlorophyll placed in 8-cm^3 vials calibrated against a mechanical pyranograph. The lifespan of the chlorophyll sensors used in the open and partly open locations was extended by shielding the vials with black tape and leaving 10- and 15-mm slits unshielded. Vials used in shady locations under fully developed canopies were unshielded. Each type of

Table 1

1971 SOLAR RADIATION IN THE OPEN AS MEASURED BY PYRANOGRAPH*

(langleys/day)

Day	April	May	June	July	Aug.	Sept.	Oct.	Nov.
1		428	[201]	548	267	120	201	54
2		508	241	468	254	388	241	54
3		602†	521	428	348	334	254	[40]
4		134	521	535	455	201	227	107
5		428	481	321	[535]†	428†	174	134
6		602†	548	535	535†	334	281	67
7	495†	535	562†	374	535†	415†	267	[201]
8	508†	535	562†	428	481	348	241	134
9	495†	575†	[628]†	548	481	160	201	80
10	481†	575†	441	535	321	107	[321]†	80
11	308	348	521	288	388	374	281	187
12	495†	415	481	535	308	374	267	147
13	508†	575†	548	455	308	401	294	174
14	[548]†	575†	334	388	401	388	308†	187
15	495†	548	321	468	535†	[441]†	308†	147
16	401	562†	548	308	535†	374	80	
17	535†	267	481	548†	535†	401	147	
18	495†	80	254	[80]	308	401	[54]	
19	187	254	308	468	348	80	160	
20	361	348	348	508	374	361	241	
21	441	562†	548	468	468	241	134	
22	508†	602†	388	281	214	147	67	
23	321	94	468	468	521†	294	80	
24	455	[67]	267	588†	535†	401	134	
25	334	227	214	388	67	134	134	
26	455	374	615†	428	187	80	134	
27	[120]	[615]†	562†	401	120	107	254	
28	241	615†	521	401	[54]	[67]	107	
29	374	575†	401	428	334	388	54	
30	187	428	415	321	481	174	254	
31		241		495	481		54	
Mean	406	429	441	434	378	282	192	120
SD‡	123	177	125	107	145	130	86	55
CV, %‡	30.3	41.4	28.3	24.8	38.4	45.9	44.9	45.6
Monthly total	12,185	13,294	13,236	13,439	11,714	8,463	5,954	3,586

*Numbers in brackets ([ ]) are maximum and minimum values.

†Daggers denote clear days.

‡Abbreviations are SD, standard deviation, and CV, coefficient of variation.

vial was calibrated separately against the pyranograph. The recording mechanical pyranograph (Model R-401 of Weather Measure Corp.) was sensitive for radiation in the wavelength range from 360 to 2500 nm, and, according to the manufacturer, its pyrex dome allows over 90% of the incident solar energy in that range to reach its black-and-white bimetallic sensor. Extraction of chlorophyll, calibration procedures, and optical-density determination essentially followed directions given by Perry and coworkers (1969).

In the field, the vials were placed vertically on the south side of aluminum stakes about 75 cm above the ground. Two vials were placed 1 m apart along one transect in each of the three forest types (Chaps. 2 and 6, this volume) at 10, 15, 25, 30, 35, 40, 50, 70, 110, and 150 m from the center of site 1 and at stations 1, 3, 5, 7, and 9 in the control area. Concurrently solar radiation was measured in the open at a nearby base station. In 1970 only chlorophyll extracts were used to measure solar radiation in the open at the West Base Station (see Chap. 2), but in 1971 and 1972 after that base station was discontinued and a new one was selected inside the fenced-in area (the new station is called East Base Station), solar radiation in the open was measured with the recording pyranograph.

Solar radiation in the forest and at the base station was measured continuously from May 19 to Nov. 30, 1970. The vials were replaced every 7 to 15 days in the forest and more frequently at the base station. In 1971 and 1972 solar radiation in the open was measured with the pyranograph continuously from early April to the end of November. In the forest it was measured with the chlorophyll extract during two 7-to-10 day periods, one each in the first and second half of each month from May to September.

In the laboratory optical densities of the exposed chlorophyll extract were measured with a spectrophotometer, and the corresponding accumulated solar energy was determined from a calibration curve relating the solar energy to optical density of the chlorophyll extract. Daily solar energy in the open was obtained by

Table 2

1972 SOLAR RADIATION IN THE OPEN AS MEASURED BY PYRANOGRAPH*
(langleys/day)

Day	April	May	June	July	Aug.	Sept.	Oct.	Nov.
1		401	535	388	401	401†	241	67
2		468	428	548	374	401†	241	27
3		588†	548	334	521†	294	80	54
4		441	602	468	[535]†	334	134	67
5	415	495	201	348	455	[428]†	160	107
6	254	267	575	468	120	94	321	54
7	441†	468	508	147	428	308	[348]†	[20]
8		615†	562	348	187	374	294	54
9		535	495	281	415	415†	321	27
10		468	642†	388	388	267	201	54
11		468	468	294	281	201	80	54
12		495	321	468	521†	267	174	67
13	120	174	334	535	401	241	348†	80
14	401	267	388	160	120	428†	134	80
15	481†	602†	[187]	[575]†	147	388	254	94
16	94	602†	562	428	267	214	281	[134]
17		535	628	[120]	468†	348	294	67
18		348	[655]†	562	308	214	134	80
19	[94]	562†	455	401	428	227	281	94
20	[495]†	294	227	334	227	187	201	80
21		441	374	294	241	388	80	107
22		562	655†	535	134	388	[27]	
23		575†	455	428	187	294	80	
24		548	481	548	201	107	281	
25		548	348	388	227	54	80	
26	94	508	495	120	[54]	174	160	
27	134	521	481	321	401	361	241	
28	267	415	214	227	428	[27]	187	
29	334	[147]	468	294	401	147	80	
30	334	[642]†	562	548	294	227	134	
31		615†		294	134		40	
Mean	283	471	462	374	313	273	191	70
SD‡	153	130	136	134	138	116	96	28
CV,‡ %	54.0	27.5	29.5	35.9	44.1	42.4	50.6	40.3
Monthly total	8,481	14,615	13,854	11,592	9,694	8,198	5,912	2,097

*Numbers in brackets ([ ]) are maximum and minimum values.
†Daggers denote clear days.
‡Abbreviations are SD, standard deviation, and CV, coefficient of variation.

planimetry on a 7-day chart from the recording pyranograph. The monthly cumulative values at each station (MCLS) were calculated as follows:

$$MCLS = \frac{LMV_1 + LMV_2}{2} \times \frac{MCLO}{PCLO}$$

where LMV_1 and LMV_2 is cumulative solar radiation measured directly by two vials located 1 m apart; MCLO is the cumulative solar radiation in the open for the entire month; and PCLO is the cumulative solar radiation in the open during the period corresponding to that of LMV.

On three occasions in the fall of 1971, the incident light was also measured with a photometer (Model 200 of Photovolt Corp.) to investigate whether these instantaneous measurements could replace the time-consuming integrating method. The light was measured only in the control area (15 stations) once on a clear day in early September when the canopies were still complete and twice in November (on a clear and a cloudy day) under leafless canopies. The readings were obtained at the same locations as the cumulative values. Sun flecks were avoided in the September measurement but were included in November when they covered a large proportion of the area.

Cumulative solar radiation values of two successive years were correlated using a linear model. Similar relationships were established between the cumulative and instantaneous light measurements.

RESULTS AND DISCUSSION

Solar Radiation in the Open

Daily solar energy was recorded on 223 days in 1971 and 219 days in 1972 from early April to mid-November (Tables 1 and 2). No daily record is available for 1970 when only cumulative solar energy was measured. The highest and lowest daily values in each month are in brackets. Their ratios ranged from 1 : 3 in June 1971 to 1 : 16 in September 1972. The variability of the data is also illustrated by coefficients of variation, which in general were higher late in the season (August to October) than in the May-to-June period. In both years the highest daily energy was determined in

Table 3

CUMULATIVE MONTHLY AND AVERAGE DAILY SOLAR RADIATION IN THE OPEN FROM 1970 TO 1972

Year	April	May	June	July	August	Sept.	Oct.	Nov.
			Cumulative Monthly Energy, langleys/month					
1970		12,450	14,270	17,884	16,425	8,333	6,812	3,229*
1971	12,185*	13,294	13,236	13,439	11,714	8,463	5,954	3,586*
1972	8,481*	14,615	13,854	11,592	9,694	8,198	5,912	2097*
Potential†	15,150	18,879	18,780	17,670	16,058	12,360	10,385	7620
			Average Daily Energy, langleys/day					
1970, mean		402	476	577	530	278	225	108*
1971, mean	406*	429	441	434	378	282	192	120*
CV,‡ %	30.3	41.4	28.3	24.8	38.4	45.9	44.9	45.6
1972, mean	283*	471	462	374	313	273	191	70*
CV,‡ %	54.0	27.5	29.5	35.9	44.1	42.4	50.6	40.3
1970–1972, mean		434	460	462	407	278	203	
Potential†	505	609	626	570	518	412	335	254
			Average Regional Solar Energy, langleys/month§					
Midwest	450	525	575	600	525	425	325	225
Northeast	350	450	525	525	450	350	250	125

*Calculations are based on incomplete measurements in the month.

†Potentials were calculated from average solar energy of clear days only, under the assumption that all days in a month are clear.

‡Abbreviation CV is coefficient of variation.

§Data are from Reifsnyder and Lull, 1965.

June (628 and 655 langleys) and the lowest in November (40 and 20 langleys).

The average daily solar radiation was calculated for each month from daily pyranograph recordings in 1971 and 1972 and from the total monthly cumulative chlorophyll value in 1970 (Table 3). The highest daily averages were 577 langleys in July 1970, 441 langleys in June 1971, and 471 langleys in May 1972. In these three years the daily averages were very similar (within ±10%) in May, June, and September and very dissimilar in July and August. The July-to-August values were substantially higher in 1970 than in either 1971 or 1972. This is consistent with subjective weather observations according to which the summer of 1970 was sunny and dry, the summer of 1971 moderately cloudy and wet, and the summer of 1972 very cloudy and wet. It is possible, however, that some artifact could be responsible for the very high values beginning in July 1970. In that year solar radiation was measured with chlorophyll extracts that could be affected not only by the two main fluxes of solar energy, diffuse light and direct solar beam, but also by light reflected from dead light-colored grass cover at the West Base Station. Moreover, this station seemed less confined by the surrounding tall vegetation than the East Base Station in which the 1971 and 1972 measurements were made. That the average solar energy data for 1971 and 1972 were reasonably similar confirms again the subjective weather observations. This similarity should be helpful in assessing the changes in incident solar radiation under canopies caused by gamma irradiation in 1972.

The 1970 values were slightly lower than average daily solar energy for the Midwest (Reifsnyder and Lull, 1965), and the 1971 and 1972 values were substantially lower (Table 3). It seems that the tabulated values for the Midwest may not be strictly applicable to the Great Lakes region, which according to Liverance and Brooks (1943) is one of two regions of the United States classified as cloudy (i.e., cloudy more than 60% of the time). The average annual number of clear and cloudy days for northern Wisconsin is about 110 and 150, respectively, about 30 and 41% (USDA, 1941). A strict comparability is not possible between those data and ours. However, on the basis of pyranograph recordings for the growing season of 1971 and 1972 (223 and 219 days, respectively), only 43 days in 1971 and 26 days in 1972 (19.6 and 11.9%, respectively) were classified as clear, 104 days in 1971 and 135 days in 1972 (46.6 and 61.6%, respectively) as partly cloudy, and 76 days in 1971 and 58 days in 1972 (34.1 and 26.5%, respectively) as cloudy (Table 4). Apparently the proportion of clear days in both years was low. In July only 2 days in 1971 and 1 day in 1972, in June 5 days in 1971 and 3 days in 1972, and in September 3 days in 1971 and 5 days in 1972 were clear. In May alone, 12 days in 1971 and 8 days in 1972 were clear. No such data are available for the generally sunny 1970 growing season.

Daily solar energies measured on clear days in each month in 1971 and 1972 were used to estimate the potential cumulative solar energy under the rather unlikely condition that all days in a given month would be clear. The data indicate that more total energy could reach these areas in May than in June but only because May has 31 days and June has 30. The average daily potential was higher in June (626 langleys) than in May (609 langleys) (Table 3). The cumulative solar energy for July and August 1970 was apparently higher than the theoretical potential energy calculated for these two months. As discussed previously, this

Table 4

NUMBER OF CLEAR, PARTLY CLOUDY, AND CLOUDY DAYS IN THE PERIOD FROM APRIL TO NOVEMBER 1971 AND 1972

Month	Number of days sampled		Clear		Partly cloudy		Cloudy	
	1971	1972	1971	1972	1971	1972	1971	1972
April	24	14	11	3	7	7	6	4
May	31	31	12	8	10	19	9	4
June	30	30	5	3	16	23	9	4
July	31	31	2	1	21	24	8	6
August	31	31	8	4	14	18	9	9
September	30	30	3	5	16	19	11	6
October	31	31	2	2	12	20	17	9
November	15	21			8	5	7	16
Total	223	219	43	26	104	135	76	58
Percentage	100	100	19.3	11.9	46.6	61.6	34.1	26.5

could have resulted from overestimation of the solar energy in 1970 when the chlorophyll extracts were used. There is another possible explanation for this discrepancy, however. An examination of the chronologically listed daily solar energies in 1971 and 1972 (Tables 1 and 2) reveals unexpected values measured on clear days. The expectation that solar energy on clear days would gradually increase until the time of summer solstice (around June 20) and then would start to decrease is not completely satisfied. High values may precede lower ones before June 20 and vice versa after that date. Thus in April 1971 the value of 548 langleys was followed by 495 langleys; in May 1971 602 was followed by 562; in July 548 was followed by 588. Similar irregularities are seen in the 1972 data (Table 2) and in comparisons of the 1971 and 1972 data for the same month. Water-vapor content was probably responsible for these irregularities (Reifsnyder and Lull, 1965). Since July and August were sunny and dry, it is possible that more energy reached the ground on clear days at this time than in the corresponding months in 1971 and 1972.

On sunny May and June days, the pyranograph registered energies of up to 1.15 langleys/min.* Energies of 1 langley/min or more were measured frequently on clear or partly cloudy days from April to August. Very low energies of 0.10 langley/min or less occurred at noon on cloudy days in October and November, but even in June or July energies as low as 0.40 langley/min were determined on cloudy days at noon. Calculated solar radiation for clear days with a solar altitude of 65° (at the summer solstice the solar altitude is $68\frac{1}{2}°$ at latitude 45°N) is about 1.32 langleys/min (Reifsnyder and Lull, 1965). The difference between this theoretical value and the measured value of 1.15 probably could be explained by the water-vapor content of the atmosphere, which was high in 1971 and 1972.

*This is probably an underestimate. William B. Fowler, Forest Hydrology Laboratory, Wenatchee, Washington, (personal communication) suggests that the pyranograph will not register short-period inputs of larger energy because of a time lag in response.

Solar Radiation Conditions Under Canopies

Cumulative solar energy determined along three transects in site 1 and the control area is summarized by transects (Figs. 1 to 4) and by four forest types (Tables 5a and 5b and Figs. 5 and 6) distinguished in a detailed sampling in site 1 and the control area (Chap. 6). Only data for the pretreatment years of 1970 and 1971 are presented here.

Solar energy trends in 1970 and 1971 remained very similar along all transects, and only seldom did the lines connecting the values at individual stations cross or deviate widely (Fig. 1 to 4). Larger absolute deviations between these two years were found at stations where more light penetrated to the ground (e.g., below openings in the canopies) especially in months like July and August, which have strikingly differing solar radiation in the open. The small absolute differences in September reflected both the generally decreasing solar radiation and small differences between the 1970 and 1971 levels in the open.

Solar radiation measurements in the open generally parallel those under the canopies, with most deviations being attributable to differences in phenology in 1970 and 1971. Thus the May solar energy in the open was higher in 1971 but the July and August values were higher in 1970, a trend that in both instances was also recorded at all 48 stations under the canopies. In June and September this consistency was absent, and some apparently contradictory relations were observed. June discrepancies (higher values under the canopy were expected in 1970) very likely resulted from differences in the phenology of developing canopies. Information on the developing tree canopies is not available at this time, but the phenology of four shrub species was delayed about 8 days in 1971 in comparison to 1970 (Zavitkovski, unpublished phenological observations). It seems likely that this delay remained through June; thus the incomplete 1971 canopies transmitted more solar radiation than the more advanced 1970 canopies.

The September discrepancy probably also resulted from differences in phenology. The 1971 solar energy in the open was slightly higher than the 1970 value, but under canopies at almost all stations the 1970 values were higher. The most likely cause for this discrepancy was the dry 1970 summer during which leaves of some species, e.g., paper birch, started to fall in August. The situation became more pronounced in September when the partially defoliated canopies transmitted more solar radiation than the essentially complete canopies of the moderately wet 1971 season. Earlier discoloration of leaves in 1970 had a similar effect because visible light interception by leaves is primarily a function of their chlorophyll content (Loomis, 1965).

The locations for the vial sensors along the three transects in site 1 were chosen mostly because other environmental factors were also measured there. A critical examination of the selected communities revealed that the original tentative classification was only partly correct and that at least four rather than three different forest types existed in site 1 and the control area (Chap. 6, this volume). When solar energies under cano-

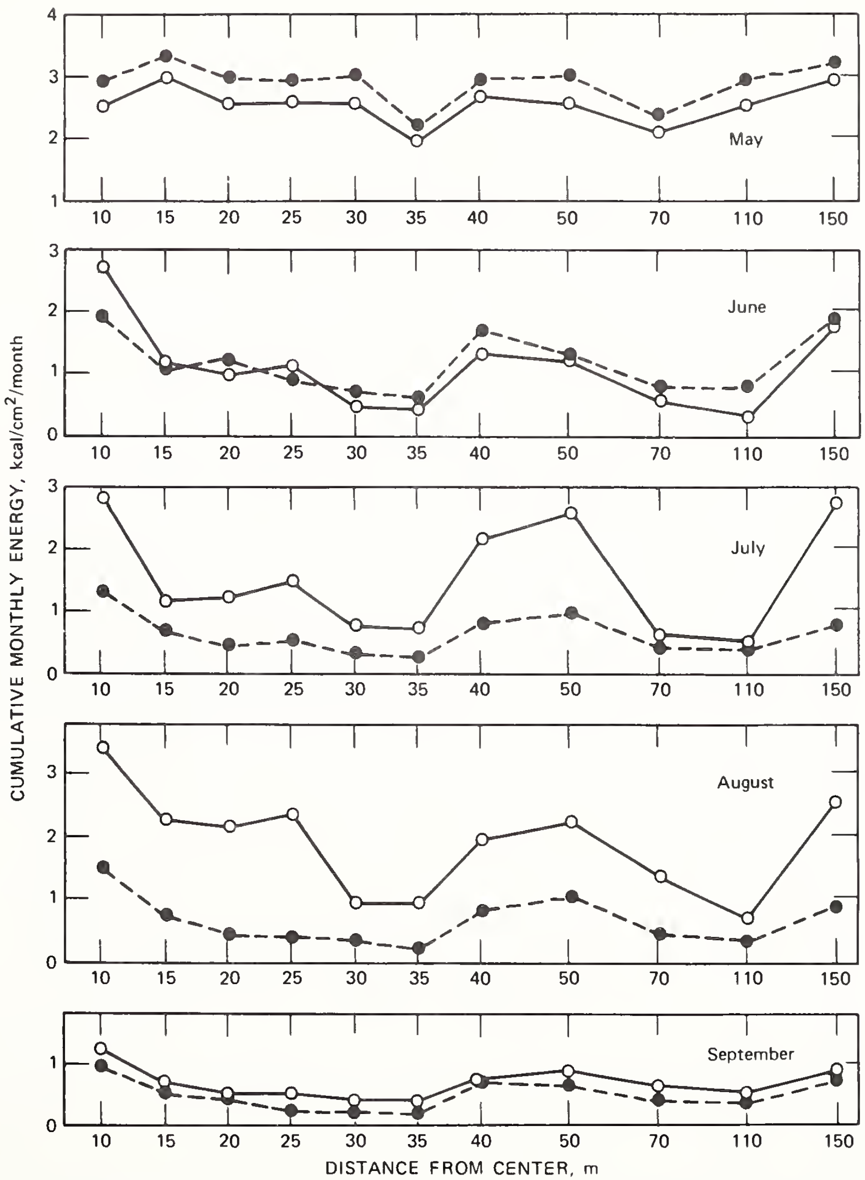

Fig. 1 Cumulative 1970 and 1971 monthly solar energy along the aspen transect in site 1. ○—○, 1970; ●---●, 1971.

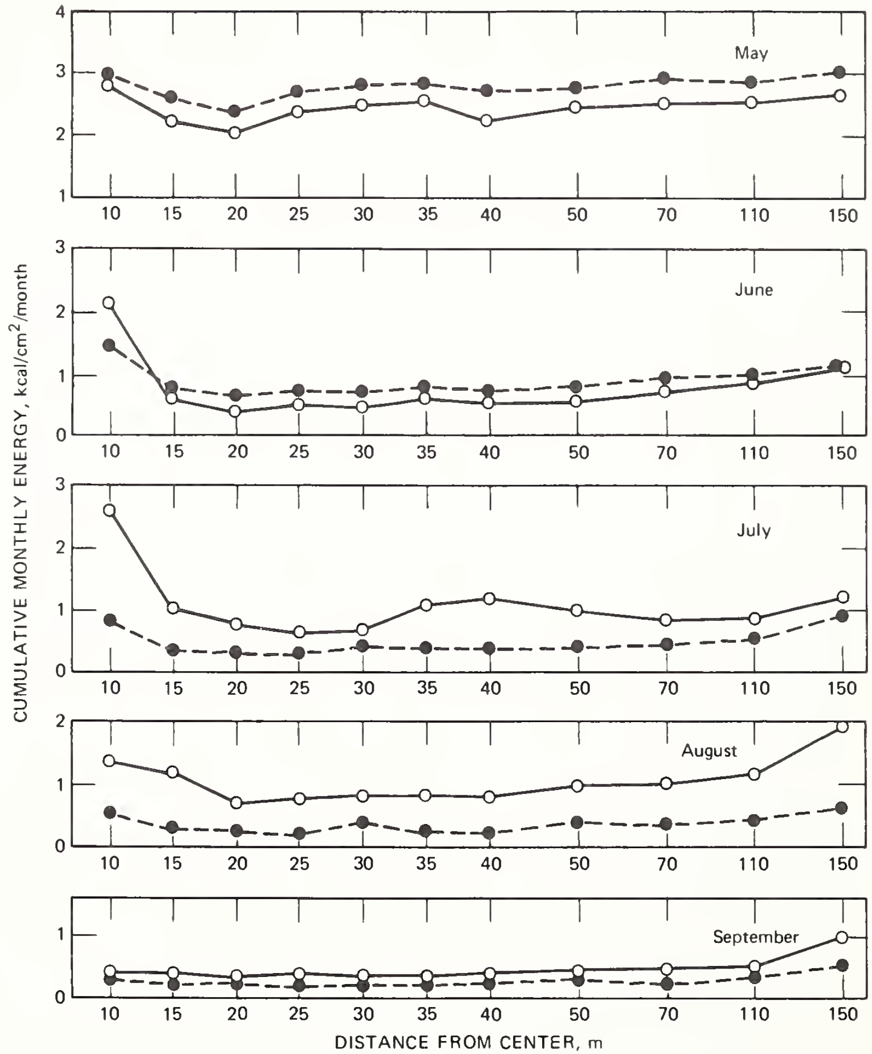

Fig. 2 Cumulative 1970 and 1971 monthly solar energy along the birch transect in site 1. ○—○, 1970; ●----●, 1971.

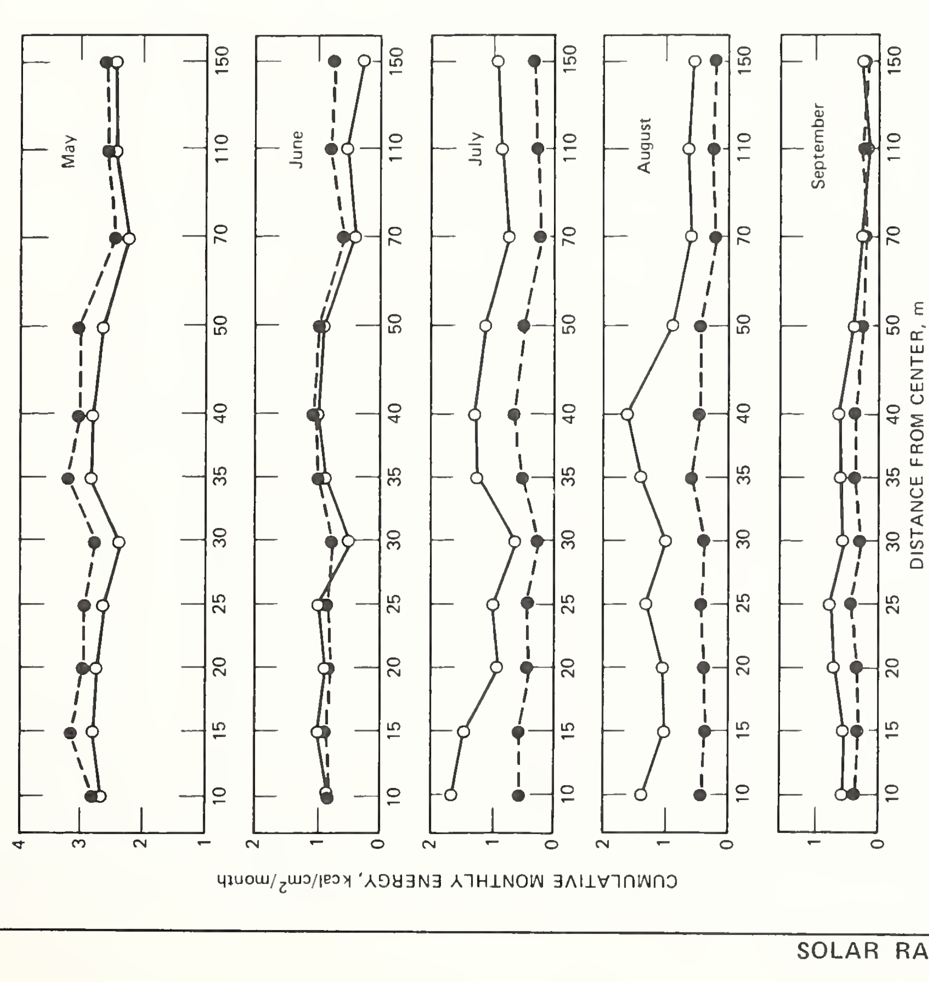

Fig. 3 Cumulative 1970 and 1971 monthly solar energy along the northern hardwood transect in site 1. ○—○, 1970; ●---●, 1971.

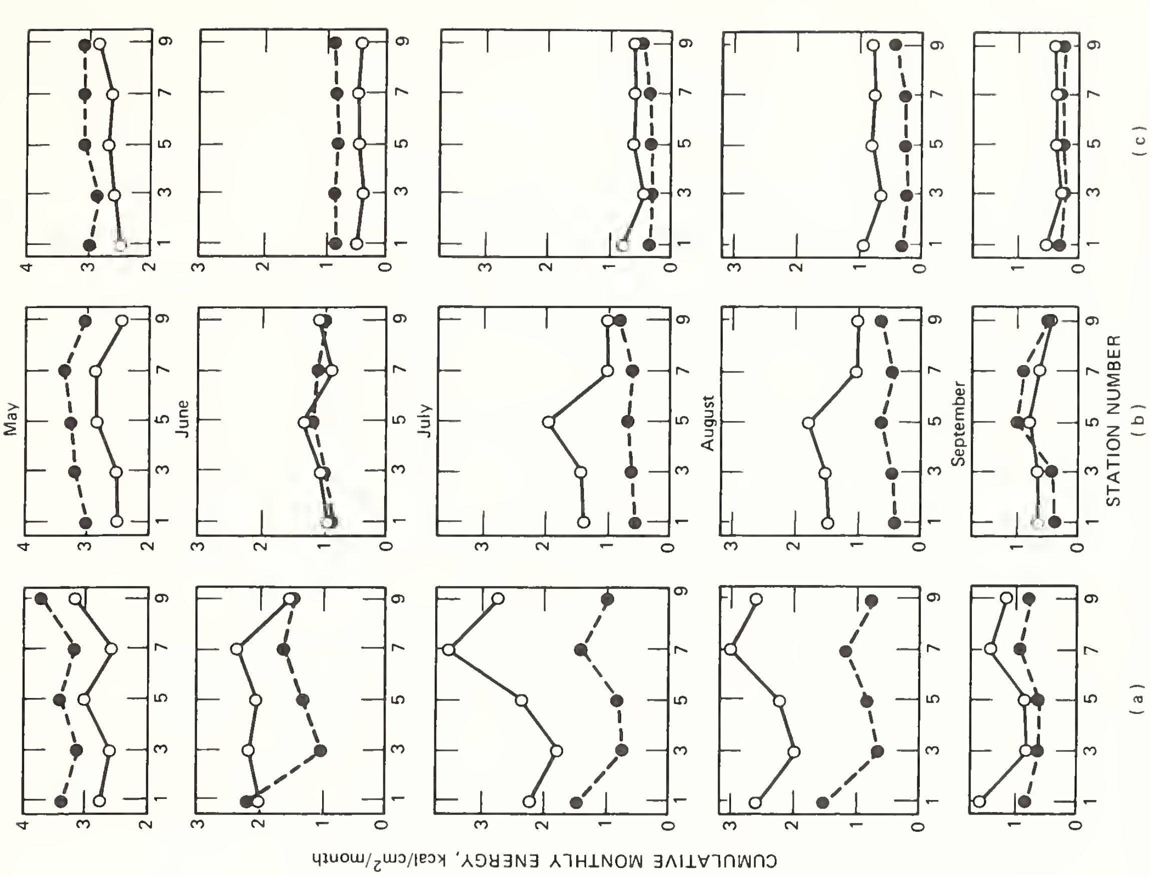

Fig. 4 Cumulative 1970 and 1971 monthly solar energy in three forest types in the control area. (a) Aspen. (b) Birch. (c) Northern hardwood. ○—○, 1970; ●---●, 1971.

Table 5a

CUMULATIVE AND RELATIVE SOLAR ENERGY UNDER CANOPIES OF FOUR FOREST TYPES IN 1970

	Month							Total	
	May	June	July	Aug.	Sept.	Oct.	Nov.	May–Sept.	July + Aug.
				Aspen (16 Recording Stations)					
Mean, langleys	2653	1376	1842	1963	828	1488	1163	8662	3805
SD*	297	751	928	808	336	345	231	2841	
CV,* %	11.2	54.6	50.4	41.2	40.6	23.2	19.9	32.8	
Percent of solar energy in the open	21.3	9.6	10.5	12.0	9.9	21.8	36.0	12.5	11.1
				Birch (8 Recording Stations)					
Mean, langleys	2586	966	1183	1356	651	1511	951	6742	2539
SD*	162	185	373	352	180	224	183	1058	
CV,* %	6.3	19.2	31.5	25.9	27.7	14.8	19.2	15.7	
Percent of solar energy in the open	20.8	6.8	6.6	8.3	7.8	22.2	29.5	9.7	7.4
				Maple–Aspen–Birch (15 Recording Stations)					
Mean, langley	2540	722	1028	1043	514	1268	1063	5847	2071
SD*	245	296	292	270	133	254	211	966	
CV,* %	9.6	41.0	28.4	25.9	25.9	20.1	19.8	16.5	
Percent of solar energy in the open	20.4	5.1	5.7	6.4	6.2	18.6	32.9	8.4	6.0
				Northern Hardwood (8 Recording Stations)					
Mean, langleys	2497	386	663	686	301	1215	875	4533	1349
SD*	171	90	148	135	100	214	74	359	
CV,* %	6.8	23.3	22.3	19.7	33.1	17.6	8.4	7.9	
Percent of solar energy in the open	20.1	2.7	3.7	4.2	3.6	17.8	27.1	6.5	3.9
In the open	12,450	14,270	17,884	16,425	8333	6812	3229	69,362	34,309
Percent of solar energy in the open†	17.9	20.6	25.8	23.7	12.0			100.0	

*Abbreviations are SD, standard deviation, and CV, coefficient of variation.
†Values for the period from May to September = 100%.

pies were averaged by forest types according to the new classification, the variability measured by coefficients of variation decreased, reflecting more homogeneous vegetation in comparison to averages by transects. The averages, plotted separately for 1970 and 1971, clearly separate the four forest types (Figs. 5 and 6). Significantly the four lines connecting monthly averages parallel each other both in 1970 and 1971, with solar radiation in the aspen and northern hardwood forest types being the highest and lowest, respectively. Statistical comparisons of solar energy among the four forest types are summarized in Table 6a for 1970 and 1971.

Solar energies under aspen canopies were not only higher but also more variable than under the other three forest types (Tables 5a, 5b, and 6a, Figs. 5 and 6). This variability was caused primarily by small openings through which direct solar beams easily penetrated to the ground, e.g., at 40 and 150 m from the site center (see Fig. 1).

Comparing trends in seasonal solar energies under canopies in 1970 and 1971, we can see a striking dissimilarity, apparently reflecting both solar energies in the open and increasing canopy density, in the July and August data (Figs. 5 and 6). In both years solar energies under canopies decreased sharply in June in response to rapidly developing canopies. In the following months, however, the 1970 and 1971 trends were strikingly different. The high solar energies in the open in July and August 1970 were also reflected under canopies; this suggests that the canopies had reached their full development in June. In contrast, under the generally uniform 1971 solar radiation conditions in the open, solar energies under canopies continued decreasing, indicating that the canopies were still developing at least through July (Fig. 6).

Along with changes in the absolute solar energies, relative values (expressed as percentages of the solar energy in the open) also changed from May to November. Although average absolute solar energies under canopies were highest in May, relatively more radiation (about one-third of that in the open) penetrated through leafless canopies in November (Table 5b). This means that even leafless canopies may absorb about two-thirds of the incident energy. Similar reductions were reported by Eber (1971) for European beech stands and by Ovington and Madgwick (1955) for a variety of broadleaf communities. Geiger (1965), sum-

Table 5b

CUMULATIVE AND RELATIVE SOLAR ENERGY UNDER CANOPIES OF FOUR FOREST TYPES IN 1971

	Month					Total		Ratio, 1970/1971	
	May	June	July	Aug.	Sept.	May–Sept.	July + Aug.	May–Sept.	July + Aug.
Aspen (16 Recording Stations)									
Mean, langleys	3056	1278	788	769	583	6474	1557	1.34	2.44
SD*	362	481	372	393	228	1639			
CV,* %	11.8	37.9	47.3	51.1	39.1	25.3			
Percent of solar energy in the open	23.0	9.7	5.9	6.6	6.9	10.8	6.2		
Birch (8 Recording Stations)									
Mean, langleys	3058	1003	637	494	532	5725	1131	1.18	2.24
SD*	165	104	139	107	256	643			
CV,* %	5.4	10.4	21.8	21.7	48.1	11.2			
Percent of solar energy in the open	23.0	7.6	4.7	4.2	6.3	9.5	4.5		
Maple–Aspen–Birch (15 Recording Stations)									
Mean, langleys	2852	788	426	371	310	4747	797	1.23	2.60
SD*	219	107	105	96	63	529			
CV,* %	7.7	13.6	24.6	25.9	20.3	11.1			
Percent of solar energy in the open	21.5	6.0	3.2	3.2	3.7	7.9	3.2		
Northern Hardwood (8 Recording Stations)									
Mean, langleys	2792	733	298	248	240	4311	546	1.05	2.47
SD*	263	89	72	67	34	474			
CV,* %	9.4	12.1	24.2	26.9	14.4	11.0			
Percent of solar energy in the open	21.0	5.5	2.2	2.1	2.8	7.2	2.2		
In the open	13,294	13,236	13,439	11,714	8463	60,146	25,153	1.15	1.36
Percent of solar energy in the open†	22.1	22.0	22.3	19.5	14.1	100.0			

*Abbreviations are SD, standard deviation, and CV, coefficient of variation.
†Values for the period from May to September = 100%.

marizing studies made in various broadleaf communities, concluded that leafless canopies may absorb about 20 to 76% of the incident light.

Very low relative values were determined in summer when the canopies reached their maximum leaf mass. In 1970 the lowest relative values (2.7 to 9.6% of the solar energy in the open) were measured in June, but in August 1971 the values were even lower (2.1 to 6.6%) (Table 5b). At some stations in the northern hardwood forest type the relative values were less than 1.5%. Aspen communities transmitted more radiation than any other community under study. The lowest relative value was 5.9% in July 1971. In 1970 the relative value never dropped below the 9.6% determined in June. In the previously mentioned beech stand, the lowest relative value determined by Eber (1971) was 3.7%. Ewel (1969) reported only 1.3% for a hammock community in Florida, and Ovington and Madgwick (1955) reported 2 to 6% for various broadleaf stands. In mixed hardwood stands of the central United States, Minckler (1961), using an integrating light meter, determined 8 to 12% of the full light. According to Reifsnyder and Lull (1965), some hardwood stands may reduce light down to 1%. In most studies light meters of various kinds were used, and absolute values were expressed either in foot-candles or kilolux, and only seldom in langleys.

More-sophisticated measurements of solar energy were made by Bjorkman and Ludlow (1972) under canopies of a Queensland rain forest. They reported that the canopies transmit relatively more energy (2.5%) in the 300 to 2400-nm range than in the visible range of 400 to 700 nm, in which only 0.48% reached the forest floor. This means that 99.52% of the total visible light can be absorbed or reflected by the canopies.

The study by Bjorkman and Ludlow is highly relevant to the present study. Chlorophyll extracts used as radiation sensors absorb very strongly in the visible range but are inefficient in other wavelengths. In the calibration process the chlorophyll sensors were compared with a pyranograph, which absorbs efficiently (more than 90%) in the 360 to 2500-nm spectrum. Bjorkman and Ludlow con-

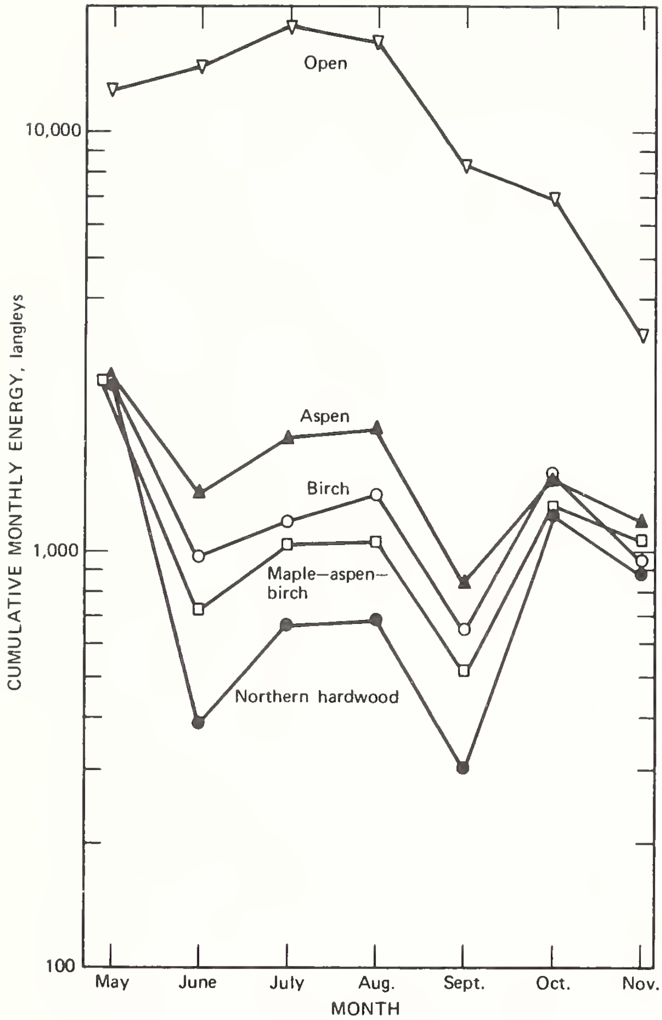

Fig. 5 Average 1970 monthly cumulative solar energy in the open and in four forest types.

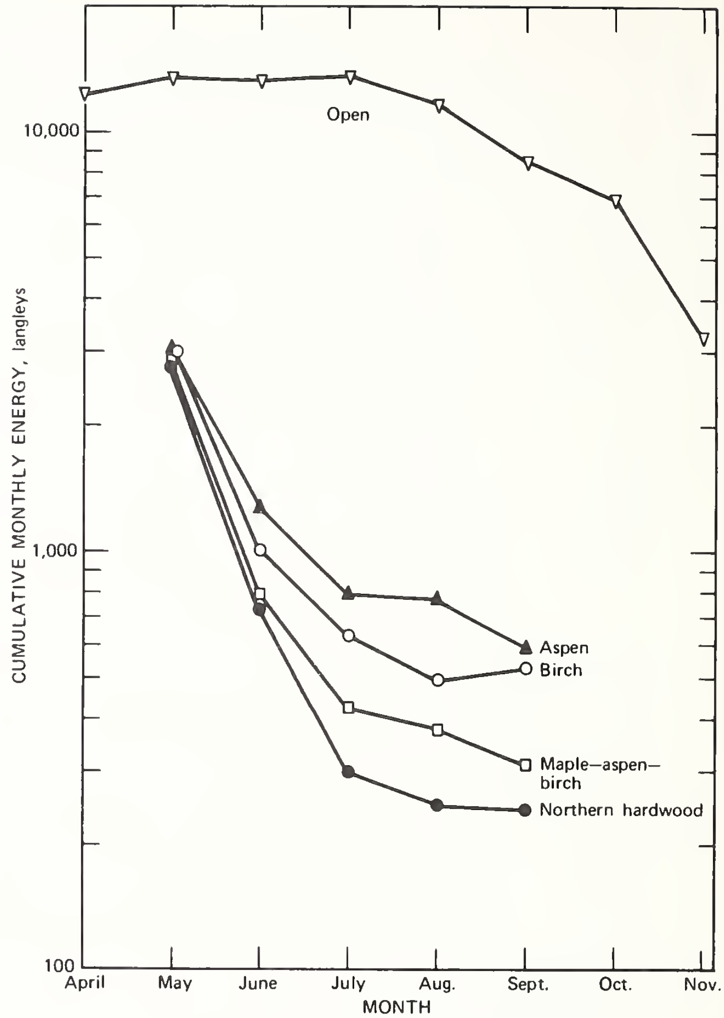

Fig. 6 Average 1971 monthly cumulative solar energy in the open and in four forest types.

cluded that on clear days under canopies all-wavelength sensors (e.g., 300 to 2400 nm) will overestimate the amount of photosynthetically active light by as much as 15 times and on overcast days by 3 times. By the same token, selective sensors (e.g., chlorophyll extracts) sensitive to the visible spectrum only will grossly underestimate the total solar energy reaching the forest floor. It would be possible to establish the relationship between energies in the visible and in the 300- to 2500-nm spectrum, but for purposes of comparing solar energy levels under canopies the present uncorrected data seem adequate and meaningful.

A comparison of the 1970 and 1971 solar energy (i.e., a ratio of 1970 to 1971) revealed that in the open 15% more energy was registered between May and September and 36% more in July and August in 1970 than in 1971. Similar comparisons made for average solar energy under canopies are expressed as 1970-to-1971 ratios separately for the May-to-September and July-to-August periods. (See Tables 5a and 5b). The May-to-September ratios were very similar to those in the open, but the values from which they were calculated were strongly influenced by the high May and June values and further confounded by irregularities in phenology. Therefore only the July-to-August ratios, which refer to a period when the canopies were fully developed, are used in the discussion. These ratios were high, indicating that 144, 124, 160, and 147% more solar energy reached the forest floor in 1970 than in 1971 in the aspen, birch, maple—aspen—birch, and northern hardwood communities, respectively, in comparison to only 36% more in the open. These comparisons indicate that canopies absorb a larger proportion of solar energy when it is scarce in the open than when it is high. This apparently contradicts conclusions reached in studies reviewed by Reifsnyder and Lull (1965) and by Geiger (1965). Waggoner, Pack, and Reifsnyder (1959), comparing solar radiation on clear and cloudy days, found that cloudiness had almost no effect on long-wave radiation transmission, but only 14% of short-wave radiation reached the ground on clear days compared with 27% on cloudy days. Ovington and Madgwick (1955) and Bjorkman and Ludlow (1972) found similar trends in their studies.

The reverse trend found in this study may have had several causes, some of which are related to phenology. The main cause probably was the incidence of sun flecks in those two years. As mentioned previously, only 10 clear days were registered during the 62-day July-to-August

Table 6

TESTS OF SIGNIFICANCE

Forest type	Aspen	Birch	Maple–aspen–birch	Northern hardwood
(a) Comparison of May-to-September Cumulative Solar Energy Among Four Forest Types in 1970				
Aspen		n.s.	1%	1%
Birch			5%	1%
Maple–aspen–birch				1%
(b) Comparison of May-to-September Cumulative Solar Energy Among Four Forest Types in 1971				
Aspen		n.s.	1%	1%
Birch			1%	1%
Maple–aspen–birch				n.s.

(c) Comparison Between 1970 and 1971 Solar Energies Within Forest Types*

Forest type	May	June	July	Aug.	Sept.	May–Sept.
Aspen	(–) 1%	(+) n.s.	(+) 1%	(+) 1%	(+) 1%	(+) 1%
Birch	(–) 1%	(–) n.s.	(+) 1%	(+) 1%	(+) 1%	(+) 1%
Maple–aspen–birch	(–) 1%	(–) 5%	(+) 1%	(+) 1%	(+) 1%	(+) 1%
Northern hardwood	(–) 1%	(–) 1%	(+) 1%	(+) 1%	(+) 1%	(+) n.s.

*The four forest types are listed in decreasing order of solar energy.

†Plus sign means that the 1970 value was greater; minus sign, that 1971 value was greater.

period in 1971; this means that the contribution of sun flecks to the total solar energy under canopies was low. Although no detailed record is available for 1970, the high cumulative solar energy values in the July-to-August period indicate a high frequency of sunny days and confirm my subjective observations. Under canopies sun flecks may contribute as much as 70% of the estimated total solar energy according to Reifsnyder and Lull (1965). Bjorkman and Ludlow (1972) calculated that two-thirds of total solar energy under canopies is contributed by sun flecks. This confirms the magnitude of the previously mentioned value.

Part of the discrepancy could have resulted from differences in the leaf biomass, especially in the aspen and maple–aspen–birch forest types, which produced slightly higher quantities of leaf litter in 1971 than 1970 (Chap. 9, this volume). It also seems likely that in 1971 the specific leaf area was larger than in 1970 because leaf thickness is positively related to solar radiation, which was substantially higher in 1970 (Logan and Krotkov, 1969; Zavitkovski, 1971). Other possible factors include leaf turgidity, especially as it affects orientation of leaves on twigs, and leaf coloration, which in 1970 was recorded already in August but very likely had started earlier before it was noticed by naked eye (Moore and Lovell, 1970). More visible light is transmitted through leaves that have lost part of their chlorophyll. It is also important to note that the lowest relative values in 1970 were recorded in June and that they subsequently increased in July and August. The July and August values were then used in comparisons with the 1971 values. Perhaps additional clues will be gained from future solar energy determinations.*

*According to William B. Fowler (personal communications) the directional placement of the sensors on the south side of aluminum stakes underestimated the diffuse north sky radiation on cloudy days and could be responsible for a large part of the discrepancy between the 1970 and 1971 solar energies under canopies.

Relations Between 1970 and 1971 Solar Energies

The relationships between the 1970 and 1971 solar energies can be inferred from their graphical representation at 48 stations along the transects (Figs. 1 to 4). Coefficients of determination were calculated to assess the relationships mathematically. The pooling of individual and cumulative values for all forest types in site 1 and the control area for each month from May to September correlated 48 pairs of values each representing a mean of two sensors located 1 m apart. As expected, the coefficients of determination were high, explaining between 69 and 89% of the variability.

Tests of significance were performed for 1970 against 1971 values separately in the four forest types (Table 6). Most comparisons yielded significantly or consistently different results, except for June values, which were very strongly affected by differences in the phenological development of canopies.

Relations Between Cumulative and Instantaneous Measurements

Instantaneous solar energy measurements generally provide less reliable data than the integrating sensors primarily because sun flecks, which provide a considerable proportion of the solar energy, are usually avoided. The main advantage of the instantaneous method is its low cost and expediency in obtaining measurements.

As expected, results from a comparison of instantaneous and cumulative light measurements indicated that for the same number of stations the instantaneous measurements were more variable than those obtained by the integrating method (Table 7). The variability probably could be reduced by increasing the number of stations at which measurements are taken, but this would defeat the original time-saving purpose for using instantaneous measurements. Also, as Minckler (1961) has pointed out, instantaneous readings must be taken several times a day because of the changing light conditions between 9 a.m. and 3 p.m., when the readings are usually taken. This condition becomes especially critical when the measurements are made on clear days and sun flecks are prominent.

Under canopies in leaf the relative values of light measured by the instantaneous method were substantially lower

Table 7

RELATION BETWEEN CUMULATIVE AND INSTANTANEOUS MEASUREMENTS OF SOLAR ENERGY

	Forest type					
	Aspen		Birch		Northern hardwood	
Station	Cumulative, langleys	Instantaneous, ft-c	Cumulative, langleys	Instantaneous, ft-c	Cumulative, langleys	Instantaneous, ft-c
			September 1971*			
1	818	405	341	210	297	110
3	649	240	442	125	212	65
5	616	185	957	325	237	70
7	899	250	889	295	250	62
9	731	275	466	165	273	82
Mean	743	271	619	224	254	78
SD†	117	82	282	85	33	19
CV,† %	15.8	30.2	45.6	37.8	12.9	25.1
Relative light values, %	8.8	5.2	7.3	4.3	3.0	1.5

	Aspen			Birch			Northern hardwood		
		Instantaneous			Instantaneous			Instantaneous	
Station	Cumulative	Cloudy	Clear	Cumulative	Cloudy	Clear	Cumulative	Cloudy	Clear
				November 1971‡					
1	1474	288	3050	930	135	2520	984	140	1565
3	1426	285	3500	1106	202	2500	805	118	1900
5	1295	210	1410	890	155	2050	921	170	1735
7	1294	232	1300	1034	175	1750	930	162	1465
9	1392	228	2800	885	182	1375	915	112	1665
Mean	1376	249	2412	969	170	2039	911	140	1666
SD†	80	36	998	97	26	492	65	26	166
CV,† %	5.8	14.3	41.4	10.0	15.1	24.1	7.2	18.3	10.0
Relative light values, %	42.6	64.2	65.1	30.0	43.8	55.1	28.2	36.1	45.0

*Instantaneous measurements were made on Sept. 20, 1971, a clear day when canopies were almost complete (average light in the open was 5250 ft-c). Cumulative values are for the month of September 1971.

†Abbreviations are SD, standard deviation, and CV, coefficient of variation.

‡Instantaneous measurements were made on Nov. 5, 1971 (a cloudy day when the average light in the open was 388 ft-c) and on Nov. 12, 1971 (a sunny day when the average light in the open was 3700 ft-c). Cumulative values are for the month of November 1970.

than those calculated from the cumulative values mainly because the sun flecks were avoided in the instantaneous measurements. The trend was reversed under leafless canopies when sun flecks occupied a large proportion of the forest floor and could not be avoided (see Table 7).

Relationships Between Basal Area or Density and Cumulative Light

Negative relationships between basal area (BA) or tree density and light have been reported by several workers for a variety of forest stands (Minckler, 1961; Reifsnyder and Lull, 1965). In the present study relationships were determined among the average cumulative solar energies measured in nine communities (three aspen and two each of birch, northern hardwood, and lowland hardwood) ranging in BA from 16.54 to 29.07 m^2/ha and in density from 1868 to 3490 trees larger than 2.5 cm dbh per hectare. The relationships were also negative, but the correlation coefficients were low and the e value (Whittaker and Woodwell, 1968) was high ($r = -0.63$, $e = 0.407$, and $r = -0.23$, $e = 0.462$ for BA–solar-energy and tree-density–solar-energy relationships, respectively). It seems unlikely that these relationships could be improved by expressing the density in some other mode, e.g., the sum of all diameters (Miller, 1959) or the sum of stem circumferences (Perry et al., 1969). Enlarging the sample size and including a wider spread of BA or densities probably would improve the relationships between these variables.

Evaluation of Light Regime Under Canopies for Regeneration and Growth

Perry and coworkers (1969), reviewing the pertinent literature on light requirements for forest regeneration, concluded that shade plants needed about 50 ft-c and sun plants 150 ft-c of light for establishment and growth. They calculated that, in terms of solar energy measured by chlorophyll extracts, this minimum light corresponds to 5 and 15 langleys/day for shade and sun plants, respectively.

Instantaneous light measurements made around noon on a clear day in September revealed that all 15 locations in the control area, including the darkest ones in the northern hardwood forest

type had enough light for successful growth of shade plants but one-third of these locations received less light than needed for the establishment and growth of sun plants (Table 7). It seems reasonable to assume that on cloudy days in September only a few locations would have enough light even for the shade plants. More light is probably available from May to August when new seedlings become established and the major proportion of growth takes place.

In terms of average cumulative solar energy, all 48 locations at which it was measured had at least 5.8 langleys/day in any month from May to September in both 1970 and 1971, and 19 stations had more than 15 langleys/day during the same period. It seems therefore that enough light existed in all locations under canopies for regeneration of shade plants, such as sugar and red maples, and in one-third of the locations for sun plants, such as aspen and paper birch. This conclusion is supported by the results of a vegetation analysis presented in Chap. 6, this volume, in which tree seedlings of various species were found in all nine communities in sufficient numbers to provide for a new forest cover if the present forest were destroyed.

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DISCLAIMER

The use of trade, firm, or corporation names in this chapter is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the U. S. Department of Agriculture of any product or service to the exclusion of others that may be suitable.

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Lichens of the Enterprise Radiation Forest

4

FREDERIC H. ERBISCH
Michigan Technological University, Houghton, Michigan

ABSTRACT

The effects of both environmental change and gamma radiation on lichen thalli in their native habitats are questionable. This study attempts to determine both the macro- and microscopic effects of these two factors on lichen thalli at the Enterprise Radiation Forest. Measurements and observations of thallus growth, configuration, and coloration; substrate temperature; thallus internal structure; and transplanted thalli are being made before irradiation for comparison with measurements and observations after the radiation treatment. It is felt that lichens closest to the source, particularly the algal component, will be most severely damaged by the radiation. The drastic environmental change caused by irradiation of the higher plants and their subsequent death or growth retardation will also affect the lichens. Which will have the greater effect and what the combined effect will be is to be determined.

The effects of gamma radiation on lichens in their natural habitats have been noted by several investigators (Brodo, 1964; Gannutz, 1968; Woodwell and Gannutz, 1967); the interpretation of these effects is contradictory, however. Brodo (1964) ascribes much of the change in the lichens, and consequently in the lichen community, to the changes in environment caused by the death and retarded growth of the higher plants. Woodwell and Gannutz (1967) and Gannutz (1968) reject this idea and indicate that the changes are directly due to the gamma radiation. Both conclusions were based on macroscopic observations at different periods in the same radiation forest. Later controlled experiments by Jones and Platt (1969) with *Parmelia conspersa* showed that on the macroscopic level environment had more effect on the lichens than did gamma radiation.

My work (Pullum and Erbisch, 1972; Erbisch, 1969a; Michigan Technological University, 1970, 1971) has shown that the lichens *Cladonia sylvatica* and *C. verticillata* are highly resistant to gamma radiation. Acute doses of 1000 kR had no macroscopic effect on podetia of *C. sylvatica*, but doses of 2000 kR caused a slight browning of podetia. On the microscopic level, however, internal damage was seen at 100 kR. Chronic irradiation at levels of approximately 500 R/day caused considerable macroscopic damage after 167 days of irradiation and one winter. Lichens receiving about 220 R/day for the same period did not appear visibly damaged, but microscopic examination showed some algal cell damage. Chronic doses of 140 R/day or less had no apparent macro- or microscopic effect even on lichens subjected to gamma radiation for two growing seasons.

The Enterprise Radiation Forest project will allow an examination of the effects of gamma radiation and climatic changes on both the macro- and microscopic characteristics of lichens in their natural habitats. The information obtained from site 1 in the radiation forest and from the control areas should give evidence of the effects on lichens of gamma radiation and environmental change, together and individually.

METHODS AND RESULTS TO DATE

Before the study and control areas were selected, a survey was made of the lichens in site 1 of the radiation forest to determine which to use in the study (Table 1).

Although the lichen population will be observed before, during, and after irradiation, small areas were selected within site 1 so that growth and macro- and microscopic changes in lichen thalli could be observed intensively.

Maple trees that had large concentrations of lichen thalli and were adjacent to the transect lines and climatic recording devices were selected as permanent "quadrats." All the tree bark quadrats selected for concentrated study had 30 or more thalli of at least two species of *Parmelia.*

Among the many lichen thalli on a tree, those selected for observation were within 1 ft of the diameter-at-breast-height (dbh) marks on the side facing the radiation source and in the same approximate area on the side of the tree away from the source. The dbh markings on the trees make it very easy to relocate lichens and serve as size and location references for tracings (Fig. 1). All lichens being studied on these trees are at approximately the same level; so climatic differences due to variations in height should not be a factor. The majority of the lichens being closely observed are *Parmelia sulcata* and *P. olivacea,* but a few thalli of *P. caperata, P. saxatilis,* and *P. arulenta* are being observed also.

Seventeen locations in site 1 were chosen for intensive study. These quadrats range from 5 to approximately 100 m from the source (Fig. 2), the majority being within 30 m of the source.

Tracings of the selected lichen thalli were made on clear acetate plastic sheets (Hale, 1954) in May 1971 and again in April 1972 to determine their growth rate. The amount of growth was found by comparing weights of paper thallus cutouts with each other and converting the paper weight to area. The average area increase of *P. sulcata* thalli was found to be 47.28 mm^2, and of *P. olivacea,* 18.07 mm^2. The growth of individual thalli was

quite variable, however. This variation appeared to be due to the organism itself and not to climatic differences because adjacent thalli often showed variances in growth. The variation in growth of *P. sulcata* appears to be associated with thallus size (Table 2). Small thalli (2 to 25 mm^2) had a 10.3% increase in size; intermediate thalli (60 to 120 mm^2) had a 31.2% increase in size; and large thalli (200 to 1000+ mm^2) had a 12.8% increase in size. Not enough thalli of *P. olivacea* were observed to determine if thallus size is a factor in growth variability. Not only does the increase in area vary but the regions of growth vary also. As shown in Fig. 3, growth does not always take place uniformly around the whole thallus.

Growth of the irradiated lichens will be studied in the same way as the unirradiated lichens to determine if radiation and the change in environment affect the overall growth of the thalli. In addition to the tracings, color photographs of each of these areas were taken and more will be taken after irradiation so that color and growth changes can be compared.

Recordings were made of the bark temperature immediately beneath some of the lichens. An Atkins 10-point recorder was used to record temperature. The stainless-steel temperature probe (½ by ⅛ in.) was inserted under the lichen through a small drilled hole. With the probe in place, the hole was sealed with grafting wax (Fig. 4). Teflon-covered cables were run from the probe to the recorder, approximately 80 m away. The ambient forest temperature was measured at the temperature-recorder site.

Thus far all the temperature measurements indicate that bark temperature lags behind the ambient temperature. The bark temperature rises and falls more slowly than the ambient temperature (Figs. 5 and 6). Bark-temperature fluctuations are likely to be more pronounced under a leafless canopy than under an intact canopy, especially in areas exposed directly to the sun. These temperature fluctuations cause climatic changes in the microhabitat, which, in turn, may affect the growth of the lichens.

In addition, as was shown in the transplant experiment, the amount of light reaching the trees also has a direct effect on the lichens. Cumulative light in the irradiated and control areas is presently being measured by the Experiment Station.

Table 1

COMMON FOLIOSE AND FRUTICOSE LICHENS AT SITE 1 OF THE ENTERPRISE RADIATION FOREST

Lichen	Habitat and occurrence	Abundance in area of concentrated study
Alectoria nidulifera Norrl.	On snag and dead *Picea* in swampy area adjacent to aspen forest	Not common
Cetraria ciliaris Ach.	On dead *Picea* in bog adjacent to aspen forest	Not present
Cladonia chlorophaea (Flk.) Spreng.	On soil bank along forest road. Over rocks and base of trees in semiopen areas	Not common
C. capitata (Michx.) Spreng.	On soil bank along forest road	Not present
C. coniocraea (Flk.) Spreng.	On soil bank and at base of trees in semiopen areas	Not common
C. consista (Ach.) Robb.	On soil along road, especially in open areas	Not common
C. cornuta (L.) Hoffm.	On soil and over rocks in semiopen areas	Moderately common along roadway
C. cristatella Tuck.	On soil and barkless logs in semiopen areas	Not common
C. gracilis (L.) Willd.	On soil, over rocks, and on debarked logs in semiopen areas	Not present
C. squamosa (Scop.) Hoffm.	On snags, soil, and rocks in open areas	Not common
C. verticillata (Hoffm.) Schaer.	On soil in semiopen areas	Not present
Evernia prunastri (L.) Ach.	On *Betula* leafless branches in semiopen exposures	Not common
Hypogymnia physodes (L.) Nyl.	On dead branches in open areas	Not common
Parmelia arulenta Tuck.	On bark of *Acer*	Moderately common
P. caperata (L.) Ach.	On bark of *Betula* and *Acer*	Moderately common
P. galbina Ach.	On bark of *Acer*	Moderately common
P. olivacea (L.) Ach.	On bark of *Populus, Acer,* and various smooth barked tree species	Common
P. saxatilis (L.) Ach.	On bark of *Betula* and *Acer*	Common
P. septentrionalis (Lynge) Ahti	On bark of *Abies balsamia* and *Acer*	Moderately common
P. sulcata Tayl.	On bark of *Betula* and *Acer*	Common
Peltigera canina (L.) Willd.	Over snag and on soil in semiopen areas	Not present
P. horizontalis (Huds.) Baumg.	Over rock and soil	Not common
P. polydactyla (Neck.) Hoffm.	Over rock, soil, and logs	Moderately common
Physcia aipolia (Ehrh.) Hampe.	On bark of *Populus* and *Acer*	Moderately common
P. ciliata (Hoffm.) DR.	On bark of *Tilia, Populus,* and *Acer*	Not common
P. orvicularis (Neck.) Poetsch.	On bark of *Populus* and *Acer*	Common
P. pulverulanta (Schreb.) Hampe	On bark of *Tilia, Populus,* and *Acer*	Common
Ramalina fastigiata (Pers.) Ach.	On bark of *Betula*	Not present
Stereocaulon saxatile Magn.	On rock in exposed areas	Not present
Usnea comosa (Ach.) Ach.	On bark of *Betula* and *Picea* snags	Not common
Xanthoria polycarpa (Ehrh.) Oliv.	On bark of *Populus*	Not common

Samples of the various *Parmelia* on the test site were collected and fixed for cytological investigation in Belling's modified Navashin fluid. The lichen material was later embedded in paraffin, sectioned, and stained (Erbisch, 1969b), and cytoplasmic and nuclear volumes were obtained. Materials of the other lichens in the area were also processed

Fig. 1 Close view of a study plot showing the temperature probe wires.

Fig. 2 View of a study plot in the Enterprise Radiation Forest, site 1, consisting of a clump of maple trees. The radiation source is at the right-hand side of the photo.

and are available for comparison studies if needed.

Cross sections of normal thalli of several species of *Parmelia* are shown in Figs. 7 to 10. Nuclear and cytoplasmic volumes for the algal symbionts are given in Table 3. Only algal nuclear and cytoplasmic volumes are given because all studies carried out in our laboratory (Michigan Technological University, 1970, 1971) indicate that the algae are the first to display damage symptoms; i.e., they are more radiosensitive than the fungal component. Radiation damage of the algal cells includes a clumping of cytoplasmic contents and chloroplastid breakdown. Little or no fungal cell damage other than a slight increase in hyphal diameter (Michigan Technological University, 1971) has been noted in any of the experiments.

To compare thallus changes due to environmental conditions with those due to radiation, we selected a site near Houghton, Mich., which approximated site 1 of the Enterprise Radiation Forest in tree type and distribution and complement of lichens. By means of a bark punch (Brodo, 1961), lichen thalli were transplanted from shady areas to sunny areas and vice versa. All bark circles were held in place with grafting wax. Some circles were moved to different positions on the same tree, and some were placed on other trees in approximately the same positions as they were originally (Michigan Technological University, 1971).

Macroscopic changes were noted in lichens transplanted from an area of shade to an area of full exposure. Thallus color changed from light gray to white, and the tips of some thallus lobes turned brown. Lichens transplanted from shaded areas to shaded areas or from sunny areas to sunny areas showed no macroscopic change. Microscopic changes of the transplanted lichens are now being studied and will be compared with changes of acutely irradiated lichens. Lichen transplants are being photographed and traced in the spring and in the fall for comparison with lichens in the irradiated forest.

Because of the varying results and interpretations by other investigators and the lack of knowledge in the area of radiation effects on lichens, it is not possible to predict the results of irradiation during one growing season. In all previous studies lichens were shown to be highly resistant to gamma radiation; therefore only the lichens nearest the source are expected to show any radiation damage. If we consider only the effects of the gamma radiation, we can predict the following results.

From data obtained in previous studies of *C. sylvatica* (Erbisch, 1969a; Michigan Technological University, 1970, 1971), I felt that little macroscopic radiation damage would be noted during the summer of 1972 but that damage would be evidenced in the following spring. The

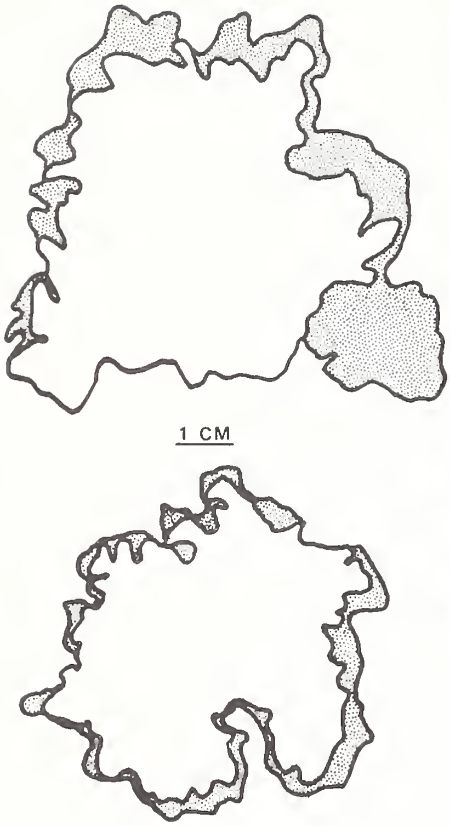

Fig. 3 Tracings of *Parmelia sulcata* thalli. The inner line indicates thallus size on May 5, 1971; the outer line indicates size on Nov. 17, 1971; and the shaded area indicates the amount of growth between May and November.

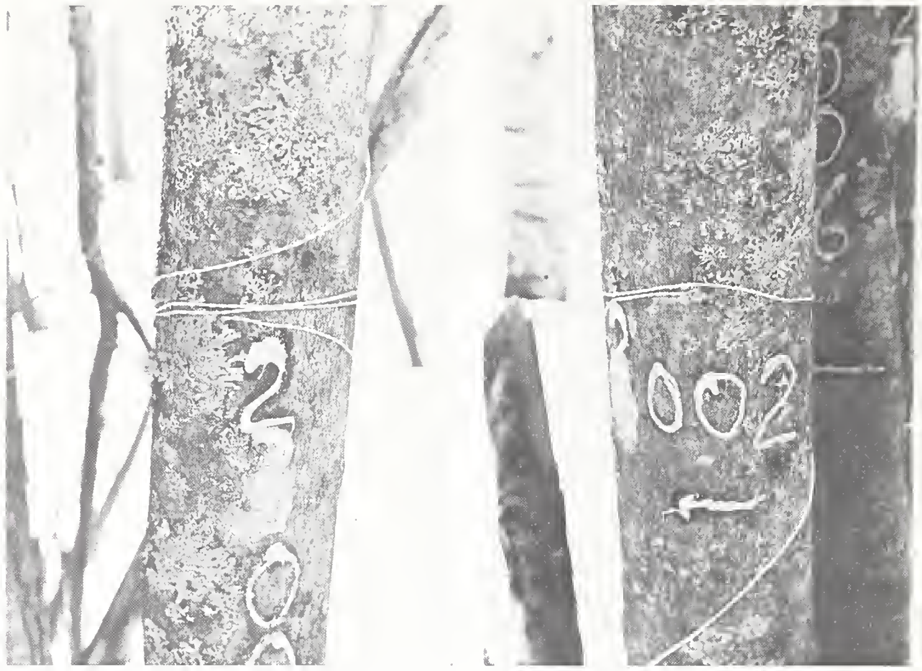

Fig. 4 Two study sites (2002 and 2003), showing the distribution of lichens and the position of the temperature probe.

Table 2

GROWTH OF REPRESENTATIVE *PARMELIA SULCATA* THALLI DURING THE PERIOD FROM MAY 1971 TO APRIL 1972

Specimen No.	Initial thallus size,* mm^2	Increase in thallus size, %	Average size increase of all thalli,† %
	Large Thalli		
18	400.0	16.8	12.8
1	460.0	16.9	
9	866.7	11.9	
13	1009.1	8.2	
	Intermediate Thalli		
2	61.8	35.0	31.2
7	72.7	32.9	
14	90.9	34.3	
16	109.7	29.6	
	Small Thalli		
19	2.4	11.1	10.3
3	11.5	10.5	

*Size was determined by weighing paper cutouts of thalli and comparing the weights with the weight of paper of known area.

†Average includes all thalli measured during the growth period.

reason for this delayed reaction is not known. *Cladonia sylvatica* in the radiation field at the North Central Forest Experiment Station showed little or no macroscopic damage while being irradiated during the entire growing season, but the next spring great changes were noted in the thalli. When the experiment was repeated, the results were duplicated; however, *C. sylvatica* clumps placed in the field in the fall after the irradiation season showed no such effects in the spring. If the species selected for study in the radiation forest react to radiation in the manner described, then those nearest the source will show the most damage and those farther away, perhaps 20 m, will show no ill effects.

Internal damage in lichens nearest the source should be noted within a month after irradiation begins. In particular, the algal component should begin to show some abnormalities; e.g., the cytoplasm may pull away from the cell wall, the chloroplastid may break up, and the cytoplasm may clump. It is also assumed that algal cells with large nuclei will show the effects sooner than those with small nuclei (Sparrow, Schairer, and Sparrow, 1963). Initially, possibly less than 1% of the algal cells will show any damage, but up to 10% of the lichens nearest the source will probably appear to be affected by the fall of the year. In this regard it is assumed that the lichen-forming algae with the largest nuclear volume will be affected earlier and more severely by the radiation.

The type of damage that will be caused by the environmental change is not known. Brodo's study (1968), which included transplanting lichen thalli, indicated that the microclimate is a limiting growth factor for some lichens. If this is so, the great climatic changes that will occur (increased light radiation, elevated temperatures, etc.) in the irradiated area as the tree canopy dies back will drastically change the microclimatic conditions

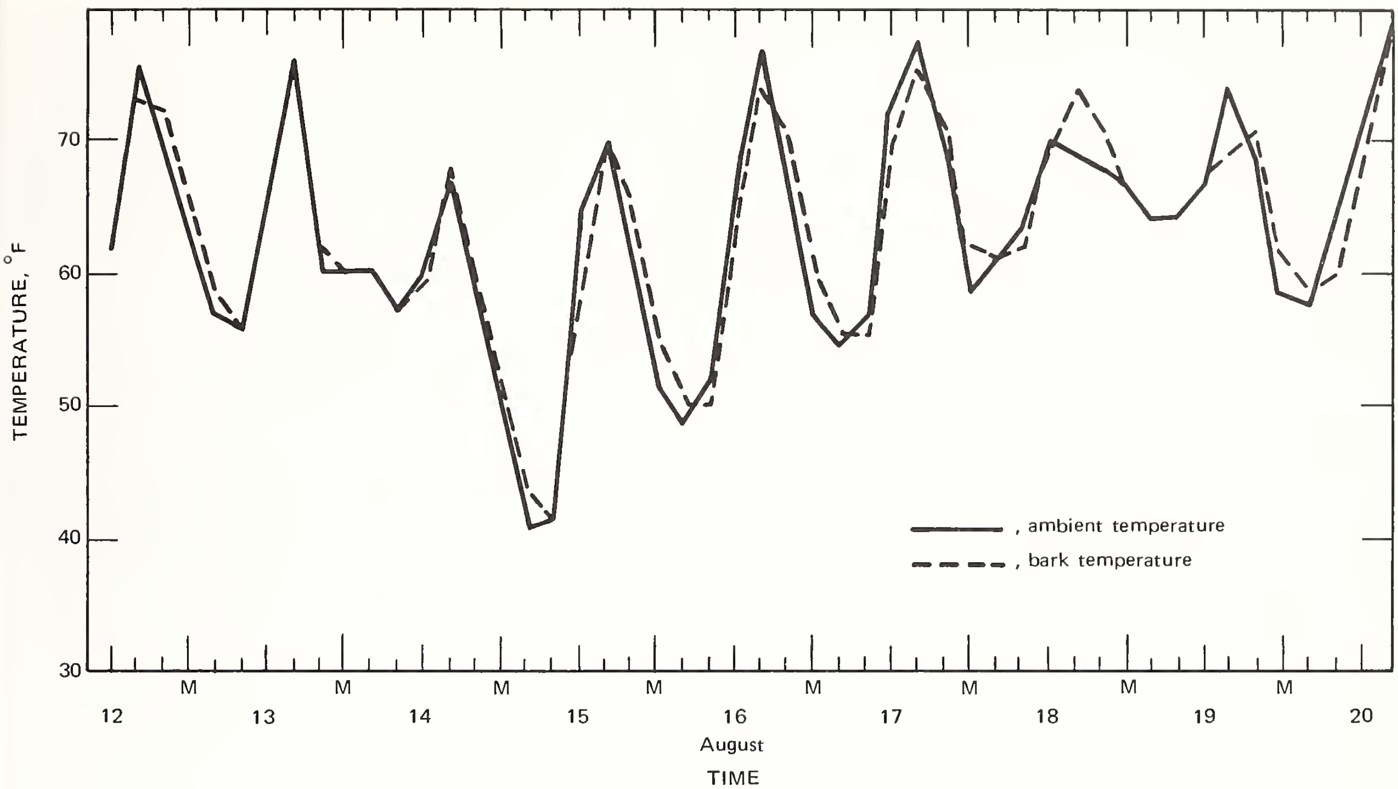

Fig. 5 Record of bark temperature (probe 3; other tree-bark probes recorded similar temperatures) compared with ambient temperature. Ambient temperature followed a fairly regular pattern during this recording period (August 12 to 20). (M = midnight.)

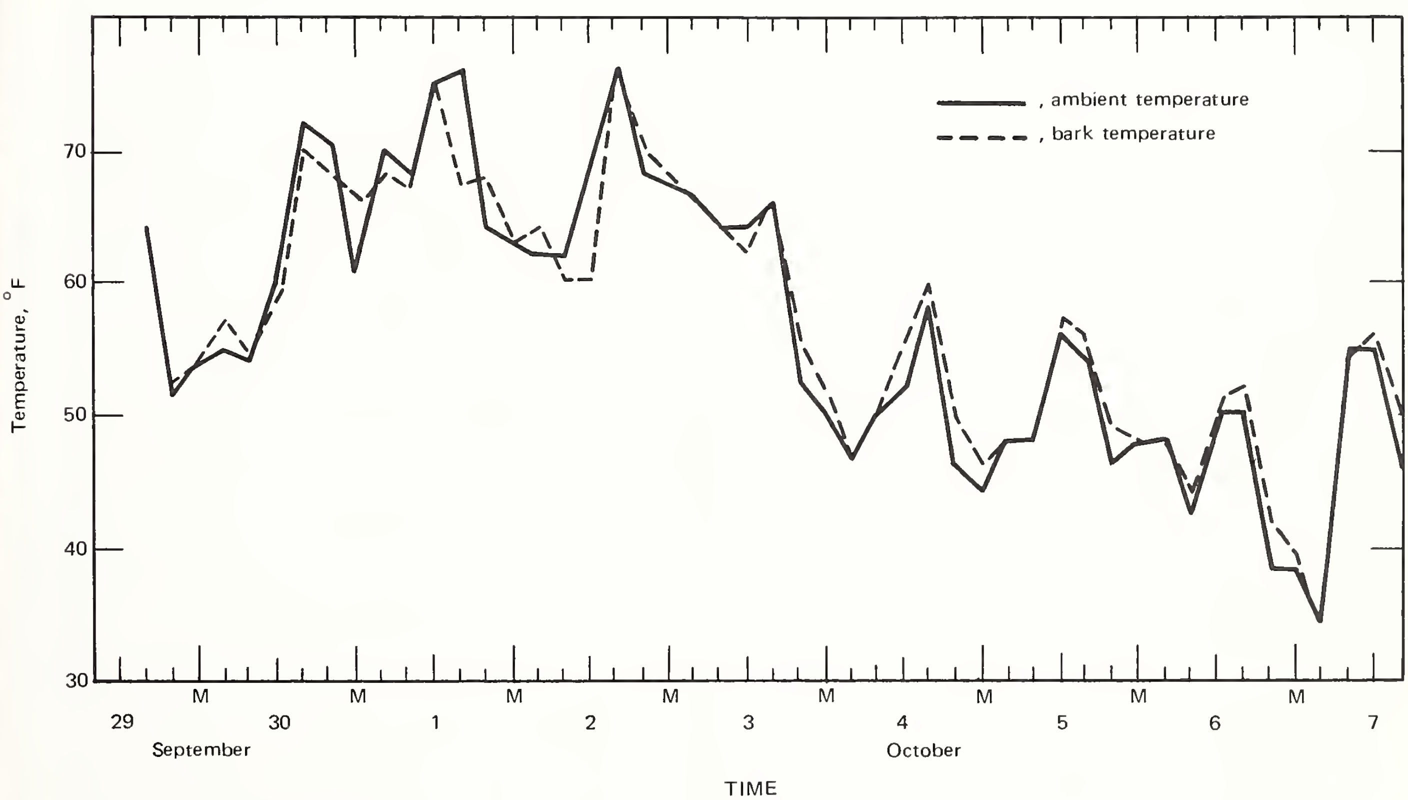

Fig. 6 Record of bark temperature (probe 3; other tree-bark probes recorded similar temperatures) compared with ambient temperature. Ambient temperature varied considerably during this recording period (September 29 to October 7). (M = midnight.)

Fig. 7 Cross section of nonirradiated thalli of *Parmelia saxatilis.*

Fig. 8 Cross section of nonirradiated thalli of *Parmelia olivacea.*

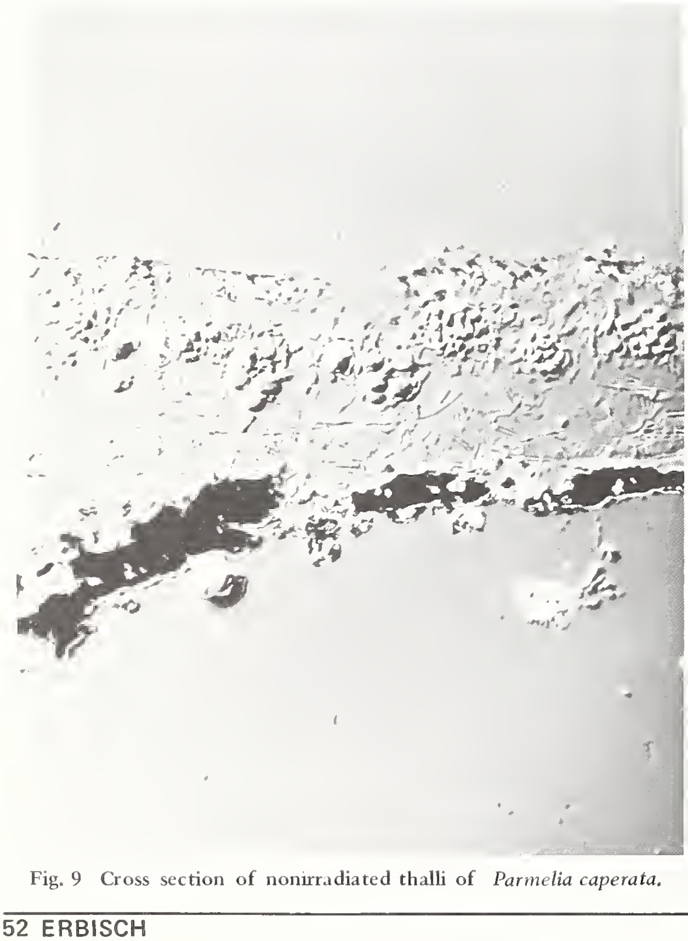

Fig. 9 Cross section of nonirradiated thalli of *Parmelia caperata.*

Fig. 10 Cross section of nonirradiated thalli of *Parmelia sulcata.*

Table 3

COMPARISON OF NUCLEAR AND CELL VOLUMES OF SEVERAL LICHEN PHYCOBIONTS

Species	Nuclear volume,* μm^3	Cell volume,* μm^3	Cell volume / Nuclear volume
Parmelia sulcata	31.01	484.47	15.62
P. olivacea	17.94	315.37	17.58
P. saxatilis	14.90	484.46	32.51
P. caperata	6.70	248.05	37.02
P. arulenta	1.98	143.55	72.50

*All cells or nuclei were assumed to be spherical.

of many of the lichens and consequently will affect growth more than radiation does. Macroscopic color changes were noted in transplants made in the Houghton area within three weeks after they were moved from shade to full exposure. The effect of the environmental change will accelerate the expected rate of radiation damage, or perhaps its effect on the lichens will completely overshadow the effects of radiation.

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Flora of the Enterprise Radiation Forest

5

JOHANNA CLAUSEN
College Ecologist, Nicolet College and Technical Institute, Rhinelander, Wisconsin

ABSTRACT

The 193 vascular plant species recorded in the Enterprise Radiation Forest are listed. Information on longevity, abundance, and existence of a voucher specimen is given for each species. The ground-cover flora of this forest most closely resembles that of the Wisconsin northern dry–mesic type described by Curtis.

Curtis (1959), in his discussion of the vegetation types of Wisconsin, describes a tension zone, or band, running northwest to southeast, which divides the state roughly in half. Within this band fall the distribution boundaries of many Wisconsin species. The same division is also evident from the work of Braun (1950). South of the tension zone, the flora is largely that of prairie and maple–basswood forest. North of the tension zone, hemlock and white pine attain importance in the forests; Braun classified the major vegetation as hemlock–white pine–northern hardwood forest. The influence of the true boreal forest just to the north of Wisconsin is apparent in many of these stands.

The Enterprise Radiation Forest, which lies in Oneida County, Wis., well to the north of the tension zone, is a second-growth forest in which cutting and probably fire have occurred.

The 193 species recorded within the transects of site 1 of the radiation area are listed in Table 1. Numbers of species present in habit categories are

Trees	28
Large shrubs	16
Ferns, club mosses, and horsetails	13
Grasses	12
Sedges and rushes	16
Forbs	108
Total	193

Fifty-two families are represented in the flora recorded for site 1. Numbers of species in each family are as follows:

Compositae	22
Cyperaceae	14
Rosaceae	14
Ericaceae	12
Gramineae	12
Liliaceae	9
Pinaceae	8
Betulaceae	6
Polygonaceae	6
Polypodiaceae	6
Ranunculaceae	5
Labiatae	5
Caprifoliaceae	4
Lycopodiaceae	4
Salicaceae	4
Aceraceae	3
Caryophyllaceae	3
Cornaceae	3
Fabaceae	3
Oleaceae	3
Orchidaceae	3
Rubiaceae	3
Saxifragaceae	3
Scrophulariaceae	3
Umbelliferae	3
Violaceae	3
Aquifoliaceae	2
Cruciferae	2
Juncaceae	2
Apocynaceae	1
Araceae	1
Araliaceae	1
Balsaminaceae	1
Campanulaceae	1
Chenopodiaceae	1
Convolvulaceae	1
Cupressaceae	1
Equisetaceae	1
Fagaceae	1
Hypericaceae	1
Iridaceae	1
Onagraceae	1
Ophioglossaceae	1
Osmundaceae	1
Oxalidaceae	1
Plantaginaceae	1
Polygalaceae	1
Primulaceae	1
Thymeleaceae	1
Tiliaceae	1
Typhaceae	1
Ulmaceae	1
Total	193

The majority of these species are perennials, and, of these, half bear their perennating buds well above the ground, as is shown in the following counts:

Perennials	
Species with perennating buds well above ground level	82
Species with perennating buds near or below ground level	81
Biennials (all with perennating buds near or below ground level)	3
Annuals	9
Uncertain classification	18
Total	193

Site 1 lies on a relatively well-drained area at the junction of three tree cover types, northern hardwood, birch, and aspen. Transects extend into each cover type. Additional transects were established on an old road running through the site. Typical bog vegetation, with a ground layer dominated by *Chamaedaphne calyculata*, *Sphagnum* sp., and other bog species, is present near the ends of the transects but is not well represented in site 1 itself.

The northern hardwood transect represents a relatively late stage in secondary

Table 1

SPECIES OF SITE 1 TRANSECTS

Species	Family	Common name	Longevity*	Laboratory number	Abundance† Forest transects	Road transects
		Trees				
Abies balsamea (L.) Mill.	Pinaceae	Balsam fir	P‡	1	F	F
Acer rubrum L.	Aceraceae	Red maple	P‡	11	A	F
Acer saccharum Marsh.	Aceraceae	Sugar maple	P‡	12	AA	X
Betula lutea Michx. f.	Betulaceae	Yellow birch	P‡	15	F	
Betula papyrifera Marsh.	Betulaceae	Paper birch	P‡	16	AA	A
Carpinus caroliniana Walt.	Betulaceae	Hornbeam	P‡	17	X	
Fraxinus americana L.	Oleaceae	White ash	P‡	18	A	X
Fraxinus nigra Marsh.	Oleaceae	Black ash	P‡	19	A	X
Fraxinus pennsylvanica Marsh.	Oleaceae	Green ash	P‡	20	X	
Larix laricina (DuRoi) K. Koch	Pinaceae	Tamarack	P‡	2	X	X
Ostrya virginiana (Mill.) K. Koch	Betulaceae	Hop hornbeam	P‡	21	A	
Picea glauca (Moench) Voss	Pinaceae	White spruce	P‡	3	X	X
Picea mariana (Mill.) BSP	Pinaceae	Black spruce	P‡	4	X	X
Pinus banksiana Lamb.	Pinaceae	Jack pine	P‡	5	X	X
Pinus resinosa Ait.	Pinaceae	Red pine	P‡	6	X	X
Pinus strobus L.	Pinaceae	White pine	P‡	7	X	X
Populus grandidentata Michx.	Salicaceae	Large tooth aspen	P‡	22	A	
Populus tremuloides Michx.	Salicaceae	Trembling aspen	P‡	23	AA	F
Prunus pensylvanica L. f.	Rosaceae	Pin cherry	P‡	24	F	
Prunus serotina Ehrh.	Rosaceae	Black cherry	P‡	25	A	
Prunus virginiana L.	Rosaceae	Chokecherry	P‡	26	F	F
Pyrus malus L.	Rosaceae	Apple	P‡	32	X	
Quercus borealis Michx. f.§	Fagaceae	Red oak	P‡	27	A	X
Sorbus americana Marsh.	Rosaceae	Mountain ash	P‡	33	X	
Thuja occidentalis L.	Cupressaceae	White cedar	P‡	8	X	X
Tilia americana L.	Tiliaceae	Basswood	P‡	29	F	X
Tsuga canadensis (L.) Carr.	Pinaceae	Hemlock	P‡	9	X	X
Ulmus americana L.	Ulmaceae	American elm	P‡	30	F	
		Large Shrubs				
Acer spicatum Lam.§	Aceraceae	Mountain maple	P‡	31	X	
Alnus rugosa (DuRoi) Spreng.	Betulaceae	Speckled alder	P‡	13	A	
Amelanchier sp.	Rosaceae	Juneberry	P‡	14	A	X
Aronia melanocarpa (Michx.) Ell.§	Rosaceae	Black chokeberry	P‡	70	X	
Cornus alternifolia L. f.§	Cornaceae	Pagoda dogwood	P‡	52	F	
Cornus stolonifera Michx.	Cornaceae	Red osier	P‡	69	X	
Corylus cornuta Marsh.§	Betulaceae	Beaked hazel	P‡	53	AA	F
Dirca palustris L.	Thymeleaceae	Leatherwood	P‡	55	F	
Ilex verticillata (L.) Gray	Aquifoliaceae	Winterberry	P‡	57	F	
Lonicera canadensis Marsh.	Caprifoliaceae	Fly honeysuckle	P‡	61	F	
Nemopanthus mucronatus (L.) Trel.	Aquifoliaceae	Mountain holly	P‡	62	F	
Ribes lacustre (Pers.) Poir.	Saxifragaceae	Swamp currant	P‡	63	F	
Rubus allegheniensis Porter	Rosaceae	Common blackberry	P‡	64	A	F
Rubus strigosus (Michx.)§	Rosaceae	Raspberry	P‡	66	F	A
Salix sp.§	Salicaceae	Willow	P‡	28	A	A
Viburnum acerifolium L.	Caprifoliaceae	Arrowwood	P‡	73	X	
		Ferns, Horsetails, and Club Mosses				
Adiantum pedatum L.	Polypodiaceae	Maidenhair fern	P	103	X	
Athyrium filix-femina (L.) Roth.§	Polypodiaceae	Lady fern	P	117	A	F
Botrychium multifidum (Gmel.) Rupr.	Ophioglossaceae	Leather grape fern	P	119	F	
Dryopteris austriaca (Jacq.) Woynar§	Polypodiaceae	Spinulose shield fern	P	147	F	
Equisetum sylvaticum L.	Equisetaceae	Wood horsetail	P	149	F	F
Lycopodium annotinum L.§	Lycopodiaceae	Club moss	P	168	F	
Lycopodium clavatum L.§	Lycopodiaceae	Running pine	P	169	A	X
Lycopodium complanatum L.§	Lycopodiaceae	Ground cedar	P	170	F	
Lycopodium obscurum L.§	Lycopodiaceae	Ground pine	P	171	AA	F
Onoclea sensibilis L.§	Polypodiaceae	Sensitive fern	P	180	F	F

Table 1 (Continued)

Species	Family	Common name	Longevity*	Laboratory number	Abundance† Forest transects	Road transects
Osmunda cinnamomea L.	Osmundaceae	Cinnamon fern	P	183	F	
Pteridium aquilinum (L.) Kuhn	Polypodiaceae	Bracken fern	P	199	AA	F
Thelypteris phegopteris (L.) Slosson.§	Polypodiaceae	Northern beech fern	P	215	X	
		Grasses				
Agrostis hyemalis (Walt.) BSP§	Gramineae	Hair grass	P	104	F	AA
Agrostis perennans (Walt.) Tuckerm.	Gramineae	Autumn bent grass	P	105	F	A
Agrostis stolonifera L.§	Gramineae	Bent grass	P	106		F
Brachyelytrum erectum (Schreb.) Beauv.§	Gramineae		P	118	A	F
Bromus ciliatus L.§	Gramineae	Fringed bromegrass	P	120	F	
Calamagrostis canadensis (Michx.) Beauv.§	Gramineae	Bluejoint	P	121	X	
Glyceria striata (Lam.) Hitchc.§	Gramineae	Fowl meadow grass	P	152	F	
Muhlenbergia racemosa (Michx.) BSP§	Gramineae	Muhly	P	242	X	X
Oryzopsis asperifolia Michx.	Gramineae	Ricegrass	P	181	AA	F
Panicum sp.	Gramineae	Panic grass	P	186	X	X
Phleum pratense L.	Gramineae	Common timothy	P	187	F	A
Poa compressa L.	Gramineae	Canada bluegrass	P	189	F	X
		Sedges and Rushes				
Carex sp.	Cyperaceae	Sedge	P	137	F	A
Carex arctata Boott§	Cyperaceae	Sedge	P	125	X	F
Carex brunnescens (Pers.) Poir.	Cyperaceae	Sedge	P	126		X
Carex crinita Lam.	Cyperaceae	Sedge	P	127	X	
Carex disperma Dew.	Cyperaceae	Sedge	P	128	X	X
Carex interior Bailey§	Cyperaceae	Sedge	P	129	F	
Carex intumescens Rudge	Cyperaceae	Sedge	P	130	F	
Carex paupercula Michx.	Cyperaceae	Sedge	P	131	F	
Carex pensylvanica Lam.§	Cyperaceae	Sedge	P	132	AA	F
Carex projecta Mackenz.	Cyperaceae	Sedge	P	133	F	
Carex retrorsa Schwein.	Cyperaceae	Sedge	P	134	F	
Carex trisperma Dew.	Cyperaceae	Sedge	P	135	F	
Carex tuckermani Boott§	Cyperaceae	Sedge	P	136	X	
Juncus tenuis Willd.§	Juncaceae	Path rush	P	162	F	AA
Luzula acuminata Raf.	Juncaceae	Wood rush	P	167	A	F
Scirpus cyperinus (L.) Kunth§	Cyperaceae	Wool grass	P	204	F	
		Forbs and Small Shrubs				
Achillea millefolium L.	Compositae	Yarrow	P	101	F	AA
Actaea alba (L.) Mill.§	Ranunculaceae	Doll's eyes	P	102	F	F
Ambrosia artemesiifolia L.	Compositae	Ragweed	A	108		F
Anaphalis margaritacea (L.) Benth. and Hook.§	Compositae	Pearly everlasting	P	109		X
Anemone quinquefolia L.	Ranunculaceae	Windflower	P	232	A	
Antennaria neglecta Greene§	Compositae	Pussytoes	P	110	F	F
Apocynum androsaemifolium L.	Apocynaceae	Dogbane	P	111	F	
Arabis glabra (L.) Bernh.	Cruciferae	Tower mustard	B	112	F	
Aralia nudicaulis L.§	Araliaceae	Wild sarsaparilla	P	113	AA	F
Aster ciliolatus Lindl.§	Compositae	Aster	P	116	F	A
Aster macrophyllus L.	Compositae	Large-leaved aster	P	114	AA	F
Aster umbellatus Mill.§	Compositae	Aster	P	115	F	AA
Bidens sp.	Compositae	Bur marigold	A or P	254		X
Calla palustris L.	Araceae	Wild calla	P	122	F	
Caltha palustris L.	Ranunculaceae	Cowslip	P	123	F	
Capsella bursa-pastoris (L.) Medic.	Cruciferae	Shepherd's purse	A or B	234		F
Cerastium vulgatum L.	Caryophyllaceae	Common mouse-ear chickweed	[illegible]	138	F	A
Chamaedaphne calyculata (L.) Moench	Ericaceae	Leatherleaf	P‡	51	F	
Chenopodium album L.	Chenopodiaceae	Lamb's-quarters	P	240		F
Chimaphila umbellata (L.) Bart.§	Ericaceae	Pipsissewa	P	139	F	
Chrysanthemum leucanthemum L.§	Compositae	White daisy	P	140	F	AA
Cicuta maculata L.	Umbelliferae	Water hemlock	P	249		X

Table 1 (Continued)

Species	Family	Common name	Longevity*	Laboratory number	Abundance† Forest transects	Road transects
Cirsium vulgare (Savi) Tenore	Compositae	Bull thistle	B	141	F	
Clintonia borealis (Ait.) Raf.§	Liliaceae	Bluebead lily	P	142	A	
Convolvulus arvensis L.	Convolvulaceae	Bindweed	P	255		X
Conyza sp.	Compositae	Horseweed	A or P	235		F
Coptis trifolia (L.) Salisb.	Ranunculaceae	Goldthread	P	143	F	
Corallorhiza maculata Raf.	Orchidaceae	Spotted coralroot	P	145	F	
Cornus canadensis L.	Cornaceae	Bunchberry	P‡	146	A	A
Diervilla lonicera Mill.	Caprifoliaceae	Bush honeysuckle	P‡	54	F	F
Epilobium glandulosum Lehm.	Onagraceae	Willow herb	P	233		A
Erigeron annuus (L.) Pers.	Compositae	Daisy fleabane	A	148		A
Fragaria virginiana Duchesne§	Rosaceae	Strawberry	P	150	F	AA
Galeopsis tetrahit L.	Labiatae	Hemp nettle	A	151	F	F
Galium tinctorium L.	Rubiaceae	Bedstraw	P	230	F	
Galium triflorum Michx.§	Rubiaceae	Sweet-scented bedstraw	P	231	F	A
Gaultheria hispidula (L.) Muhl.§	Ericaceae	Snowberry	P	72	X	
Gaultheria procumbens L.§	Ericaceae	Wintergreen	P‡	56	A	F
Gnaphalium uliginosum L.	Compositae	Cudweed	A	153	F	F
Habenaria sp.	Orchidaceae		P	243		F
Hepatica americana (DC.) Ker.	Ranunculaceae	Hepatica	P	155	X	
Hieracium aurantiacum L.	Compositae	King devil	P	157	F	A
Hieracium scabrum Michx.	Compositae	Hawkweed	P	158	F	F
Impatiens biflora Willd.	Balsaminaceae	Spotted touch-me-not	A	160	F	F
Iris versicolor L.§	Iridaceae	Blue flag	P	161	F	X
Kalmia polifolia Wang.§	Ericaceae	Bog laurel	P‡	58	F	
Lactuca biennis (Moench) Fern.	Compositae	White lettuce	A or B	163	F	X
Lactuca canadensis L.	Compositae	Lettuce	A or B	164	F	X
Ledum groenlandicum Oeder§	Ericaceae	Labrador tea	P‡	59	F	
Linnaea borealis L.§	Caprifoliaceae	Twinflower	P	60	F	
Lobelia inflata L.§	Campanulaceae	Indian tobacco	A	166		F
Lychnis alba Mill.§	Caryophyllaceae	White campion	B or P	241		F
Lycopus uniflorus Michx.	Labiatae	Water horehound	P	172	F	F
Maianthemum canadense Desf.§	Liliaceae	Wild lily of the valley	P	173	AA	X
Malaxis unifolia Michx.	Orchidaceae	Adder's mouth	P	263	X	
Melampyrum lineare Desr.§	Scrophulariaceae	Cowwheat	A	174	F	
Mitchella repens L.	Rubiaceae	Partridgeberry	P	175	F	X
Mitella diphylla L.	Saxifragaceae	Bishop's mitrewort	P	176	X	
Mitella nuda L.	Saxifragaceae	Bishop's-cap	P	177	X	
Monotropa hypopithys L.	Ericaceae	Pinesap		178	X	
Monotropa uniflora L.	Ericaceae	Indian pipe		179	X	
Osmorhiza claytoni (Michx.) Clarke	Umbelliferae	Sweet cicely	P	182	X	
Oxalis europaea Jord.	Oxalidaceae	Sheep sorrel	A or P	184	X	A
Plantago major L.	Plataginaceae	Plaintain	A or P	188	X	AA
Polygala paucifolia Willd.	Polygalaceae	Flowering wintergreen	P	191	F	
Polygonatum pubescens (Willd.) Pursh§	Liliaceae	Solomon's seal	P	192	F	
Polygonum sp.	Polygonaceae	Smartweed	A or P	239		F
Polygonum cilinode Michx.	Polygonaceae	Bindweed	P	193	F	F
Polygonum persicaria L.	Polygonaceae	Smartweed	A	194	X	A
Polygonum scandens L.	Polygonaceae	False buckwheat	P	229	X	
Potentilla norvegica L.	Rosaceae	Cinquefoil	A, B or short-lived P	195		A
Potentilla palustris (L.) Scop.	Rosaceae	Cinquefoil	P	252		X
Prenanthes alba L.§	Compositae	Rattlesnake root	P	197	F	F
Prunella vulgaris L.	Labiatae	Self-heal	P	198	X	AA
Pyrola rotundifolia L.§	Ericaceae	Shinleaf	P	200	A	X
Pyrola virens Schweigger§	Ericaceae	Shinleaf	P	201	A	X
Rubus pubescens Raf.§	Rosaceae	Dwarf blackberry	P	65	F	F
Rumex acetosella L.	Polygonaceae	Red sorrel	A or P	245		X
Rumex crispus L.	Polygonaceae	Sour dock		203	X	X
Scutellaria galericulata L.	Labiateae	Skullcap	P	205	X	

Table 1 (Continued)

Species	Family	Common name	Longevity*	Laboratory number	Abundance† Forest transects	Road transects
Scutellaria lateriflora L.	Labiateae	Mad-dog skullcap	P	206	F	
Sium suave Walt.	Umbelliferae	Water parsnip	P	207	X	
Smilacina racemosa (L.) Desf. §	Liliaceae	False Solomon's seal	P	208	X	
Smilacina trifolia (L.) Desf.	Liliaceae	Three-leaved false Solomon's seal	P	209	X	
Solidago spp.	Compositae	Goldenrod	P	211	F	AA
Solidago flexicaulis L.	Compositae	Goldenrod	P	250	X	
Solidago graminifolia (L.) Salisb. §	Compositae	Goldenrod	P	210	X	F
Spiraea alba DuRoi	Rosaceae	Meadowsweet	P	71	X	
Stellaria graminea L.	Caryophyllaceae	Chickweed	P	212		X
Streptopus roseus Michx. §	Liliaceae	Twisted-stalk	P	213	F	
Taraxacum officinale Weber	Compositae	Common dandelion	P	214	X	
Triadenum fraseri (Spach) Gleason §	Hypericaceae	Marsh St.-John's-wort	P	251		X
Trientalis borealis Raf. §	Primulaceae	Starflower	P	216	A	
Trifolium pratense L.	Fabaceae	Red clover	B or short-lived P	217		F
Trifolium procumbens L.	Fabaceae	Hop clover	A	237		F
Trifolium repens L.	Fabaceae	White clover	P	218	F	AA
Trillium grandiflorum (Michx.) Salisb. §	Liliaceae	White trillium	P	219	F	
Typha latifolia L.	Typhaceae	Cattail	P	256		X
Uvularia grandiflora Sm. §	Liliaceae	Large-flowered bellwort	P	259	X	
Uvularia sessilifolia L.	Liliaceae	Bellwort	P	220	F	
Vaccinium myrtilloides Michx.	Ericaceae	Velvet-leaf viburnum	P‡	67	F	X
Vaccinium oxycoccos L.	Ericaceae	Small cranberry	P	74	X	
Verbascum thapsus L.	Scrophulariaceae	Mullein	B	221		X
Veronica serpyllifolia L.	Scrophulariaceae	Thyme-leaved speedwell	P	222	F	F
Viola incognita var. Forbesii Brainerd	Violaceae	Wild white violet		224	A	AA
Viola pubescens Ait.	Violaceae	Downy yellow violet		223	A	
Viola papilionacea Pursh	Violaceae	Meadow violet		225	X	X
Waldsteinia fragarioides (Michx.) Tratt. §	Rosaceae	Barren strawberry	P	228	X	

*Abbreviations are P, perennial; B, biennial; and A, annual.
†Abundance was estimated from inspection and frequency records. The symbols are AA, very abundant; A, abundant; F, few; and S, very few.
‡Perennating buds are well above ground.
§Voucher specimen is on file in the laboratory herbarium.

succession toward the northern dry–mesic climax forest. The aspen and birch transects represent earlier stages of the same succession.

Although three tree cover types can be distinguished at site 1, the ground cover is relatively similar throughout. *Aralia nudicaulis, Aster macrophyllus, Carex pensylvanica, Maianthemum canadense, Oryzopsis asperifolia,* and *Pteridium aquilinum* are the most plentiful species. Inspection of the vegetation tables of Curtis (1959) shows that this ground cover is most similar to that of the northern dry–mesic forests of Wisconsin but has much in common with boreal forests.

The northern mesic climax forest vegetation in this north central area of Wisconsin is dominated by sugar maple, hemlock, yellow birch, and basswood. Xeric climax forest stands in this region are dominated by white pine, red pine, and jack pine. In dry–mesic stands varying mixtures of these tree species dominate. Ground-layer vegetation is similar in northern mesic and northern dry–mesic forests, but *Anemone quinquefolia, Aster macrophyllus, C. pensylvanica, Diervilla lonicera, Mitchella repens, O. asperifolia, P. aquilinum, Trientalis borealis* and *Uvularia sessilifolia* increase in importance with increasing dryness. As is typical for mesic forests of this portion of Wisconsin, spring-flowering ephemerals are not an important part of the flora of site 1.

Carex pensylvanica appears to be more abundant in site 1 than in the typical northern dry–mesic forest. This species grows well on dry rocky soil and may be favored by such disturbances as cutting, burning, and bulldozing. As is true of many of the other ground-cover species in site 1, this sedge seldom flowers under the forest cover but propagates mainly by vegetative spread.

Forests with true boreal climax tree cover are not well represented in Wisconsin, being mainly limited to the extreme northwest corner of the state. Ground cover of these forests, as reported by Curtis, is in many respects intermediate between that of the northern dry–mesic forests of Wisconsin and the true boreal forests of more northern regions. Elsewhere in the state an abundance of the boreal tree dominants *Abies balsamea* and *Picea glauca* usually indicates secondary succession following recent disturbance.

Boreal and northern dry–mesic forests in Wisconsin show much similarity in ground vegetation, both having abundant amounts of *Anemone quinquefolia, Aralia nudicaulis, Aster macrophyllus, Maianthemum canadense, O. asperifolia, Pteridium aquilinum,* and *T. borealis.* The following species, however, are much better represented in boreal than in dry–mesic forests: *Clintonia borealis, Cornus canadensis, Dryopteris austriaca, Fragaria virginiana, Galium triflorum, Linnaea borealis, Mitella nuda, Rubus pubescens, Streptopus roseus,* and *Viola incognita. Clintonia borealis, Cornus canadensis,* and *V. incognita* are well represented in the Enterprise transects, but none of the other listed species are.

The old logging road that runs through site 1 supports a weed vegetation drawn from various sources, some contiguous and others distant. The following list includes highly abundant and abundant species under the community type from which they most probably emigrated:

Boreal and northern Wisconsin mesic or dry–mesic forests

- *Betula papyrifera*
- *Cornus canadensis*
- *Galium triflorum*
- *Fragaria virginiana*
- *Rubus strigosus**
- *Viola incognita*

Northern wet and bog forests

- *Agrostis hyemalis*
- *Agrostis perennans*
- *Aster ciliolatus*
- *Aster umbellatus*
- *Epilobium glandulosum*

Lake beaches

- *Cerastium vulgatum**

Table 2

SPECIES FOUND IN RADIATION AREA OUTSIDE SITE 1

Species	Family	Common name	Longevity*
	Large Shrubs		
Physocarpus opulifolius (L.) Maxim.	Rosaceae	Ninebark	P
Prunus pumila L.	Rosaceae	Sand cherry	P
Rhus typhina L.	Anacardiaceae	Staghorn sumac	P
Ribes cynosbati L.	Saxifragaceae	Prickly gooseberry	P
Ribes glandulosum Grauer	Saxifragaceae	Skunk currant	P
Rosa carolina L.	Rosaceae	Pasture rose	P
Salix humilis Marsh.	Salicaceae	Upland willow	P
Salix pyrifolia Anderss.	Salicaceae	Balsam willow	P
Sambucus sp.	Caprifoliaceae	Elder	P
	Ferns, Club Mosses and Horsetails		
Dryopteris cristata (L.) Gray	Polypodiaceae	Crested shield fern	P
Gymnocarpium dryopteris (L.) Newm.†	Polypodiaceae	Oak fern	P
Lycopodium lucidulum Michx.	Lycopodiaceae	Shining club moss	P
Osmunda claytoniana L.	Osmundaceae	Interrupted fern	P
Thelypteris palustris Schott.	Polypodiaceae	Marsh fern	P
	Grasses		
Agropyron repens (L.) Beauv.	Gramineae	Quack grass	P
Bromus kalmii Gray	Gramineae	Bromegrass	P
Cinna latifolia (Trev.) Griseb.†	Gramineae	Drooping woodreed	P
Festuca octoflora Walt.†	Gramineae	Fescue	A
Glyceria canadensis (Michx.) Trin.	Gramineae	Rattlesnake grass	P
Glyceria pallida (Torr.) Trin.	Gramineae	Manna grass	P
Phalaris arundinacea L.	Gramineae	Reed canary grass	P
Poa interior Rydb.	Gramineae	Inland bluegrass	P
Poa pratensis L.	Gramineae	Kentucky bluegrass	P
Poa saltuensis Fern & Wieg.	Gramineae	Bluegrass	P
Poa wolfi Scribn.	Gramineae	Bluegrass	P
Schizachne purpurascens (Torr.) Swallen	Gramineae	False melic	P
	Sedges and Rushes		
Carex arcta Boott†	Cyperaceae	Sedge	P
Carex debilis Michx.	Cyperaceae	Sedge	P
Carex lacustris Willd.	Cyperaceae	Sedge	P
Carex lasiocarpa Ehrh.	Cyperaceae	Sedge	P
Carex leporina L.	Cyperaceae	Sedge	P
Carex normalis Mackenz.	Cyperaceae	Sedge	P
Carex oligosperma Michx.	Cyperaceae	Sedge	P
Carex pauciflora Lightf.	Cyperaceae	Sedge	P
Carex rostrata Stokes, var. utriculata (Boott) Bailey†	Cyperaceae	Sedge	P
Carex scoparia Schkuhr, var. *moniliformis* Tuckerm.	Cyperaceae	Sedge	P
Carex stipata Muhl.	Cyperaceae	Sedge	P
Dulichium arundinaceum (L.) Britt.†	Cyperaceae	Three-way sedge	P
Eriophorum angustifolium Honckeny	Cyperaceae	Cotton grass	P
Eriophorum spissum Fern.	Cyperaceae	Cotton grass	P
Eriophorum tenellum Nutt.	Cyperaceae	Cotton grass	P
Eriophorum virginicum L.	Cyperaceae	Tawny cotton grass	P
Juncus effusus L.	Juncaceae	Soft rush	P
Rhynchospora alba (L.) Vahl	Cyperaceae	Beak rush	P
Scheuchzeria palustris L.	Juncaginaceae		P
Scirpus atrovirens Willd.	Cyperaceae	Bulrush	P
	Forbs and Small Shrubs		
Agrimonia striata Michx.	Rosaceae	Harvest-lice	P
Andromeda glaucophylla Link†	Ericaceae	Bog rosemary	P
Anemone virginiana L.	Ranunculaceae	Thimbleweed	P
Aquilegia canadensis L.	Ranunculaceae	Wild columbine	P
Aralia hispida Vent.	Araliaceae	Bristly sarsaparilla	P

Table 2 (Continued)

SPECIES FOUND IN RADIATION AREA OUTSIDE SITE 1

Species	Family	Common name	Longevity*
Arisaema triphyllum (L.) Schott	Araceae	Small jack-in-the-pulpit	P
Asclepias syriaca L.	Asclepiadaceae	Common milkweed	P
Aster puniceus L.	Compositae	Aster	P
Aster simplex Willd.	Compositae	Aster	P
Barbarea vulgaris R. Br.	Cruciferae	Yellow rocket	P
Cicuta bulbifera L.	Umbelliferae	Water hemlock	P
Circaea alpina L.	Onagraceae	Enchanter's nightshade	P
Cirsium muticum Michx.	Compositae	Swamp thistle	B
Comandra richardsiana Fern.†	Santalaceae	Bastard toadflax	
Corallorhiza trifida Chatelain	Orchidaceae	Coralroot	P
Cryptotaenia canadensis (L.) D.C.	Umbelliferae	Honewort	P
Cypripedium acaule Ait.	Orchidaceae	Stemless lady's-slipper	P
Drosera rotundifolia L.	Droseraceae	Round-leaved sundew	P or B
Epigaea repens L.†	Ericaceae	Trailing arbutus	P
Epilobium adenocaulon (Haussk.)	Onagraceae	Willow herb	P
Epilobium angustifolium L.	Onagraceae	Great willow herb	P
Epilobium leptophyllum Raf.	Onagraceae	Willow herb	P
Erigeron strigosus Muhl.	Compositae	Daisy fleabane	A
Eupatorium perfoliatum L.	Compositae	Boneset	P
Galium asprellum Michx.	Rubiaceae	Bedstraw	P
Galium palustre L.	Rubiaceae	Bedstraw	P
Geum aleppicum Jacq.	Rosaceae	Avens	P
Geum canadense Jacq.	Rosaceae	Avens	P
Habenaria clavellata (Michx.) Spreng.	Orchidaceae		P
Habenaria obtusata (Pursh) Richards.	Orchidaceae	Blunt-leaf orchid	P
Hieracium longipilum Torr.	Compositae	Hawkweed	P
Hydrophyllum virginianum L.	Hydrophyllaceae	Waterleaf	P
Hypericum boreale (Britt.) Bickn.†	Hypericaceae	St.-John's-wort	P
Hypericum canadense L.	Hypericaceae	St.-John's-wort	P
Hypericum pyramidatum Ait.	Hypericaceae	Great St.-John's-wort	P
Leonurus cardiaca L.	Labiatae	Motherwort	P
Linaria vulgaris Hill†	Scrophulariaceae	Butter-and-eggs	P
Menyanthes trifoliata L.	Gentianaceae	Buckbean	P
Myrica asplenifolia L.	Myrtaceae	Sweet fern	P
Naumburgia thyrsiflora (L.) Duby	Primulaceae	Tufted loosestrife	P
Oxalis violaceae L.	Oxalidaceae	Wood sorrel	P
Pilea pumila (L.) Gray	Urticaceae	Clearweed	
Polygonum aviculare L.	Polygonaceae	Knotweed	A
Polygonum punctatum Ell.	Polygonaceae	Smartweed	A
Polygonum sagittatum L.†	Polygonaceae	Arrowleaved tearthumb	
Potentilla recta L.†	Rosaceae	Cinquefoil	P
Potentilla simplex Michx.	Rosaceae	Old-field cinquefoil	
Pyrola elliptica Nutt.	Ericaceae	Shinleaf	P
Pyrola secunda L.	Ericaceae	One-sided pyrola	P
Ranunculus abortivus L.	Ranunculaceae	Kidneyleaf buttercup	
Ranunculus acris L.†	Ranunculaceae	Common buttercup	P
Ranunculus pensylvanicus L. f.	Ranunculaceae	Bristly crowfoot	A or P
Sanicula marilandica L.†	Umbelliferae	Black snakeroot	B or P
Sarracenia purpurea L.	Sarraceniaceae	Pitcher plant	P
Satureja vulgaris (L.) Fritsch	Labiatae	Wild basil	P
Scrophularia marilandica L.	Scrophulariaceae	Figwort	P
Solidago canadensis L.	Compositae	Goldenrod	P
Solidago hispida Muhl.	Compositae	Goldenrod	P
Solidago uliginosa Nutt.	Compositae	Goldenrod	P
Spiraea tomentosa L.	Rosaceae	Hardhack	P
Spiranthes cernua (L.) Richard	Orchidaceae	Common ladies' tresses	P
Spiranthes gracilis (Bigel.) Beck	Orchidaceae	Slender ladies' tresses	P
Trifolium agrarium L.	Fabaceae	Hop clover	A
Vaccinium angustifolium Ait.†	Ericaceae	Low sweet blueberry	P
Vaccinium myrtilloides Michx.	Ericaceae	Velvet-leaf viburnum	P

*Abbreviations are P, perennial; B, biennial; and A, annual.
†Voucher specimen is on file in the laboratory herbarium.

Bracken grasslands
*Hieracium aurantiacum**
Railroad yards:
*Polygonum persicaria**
Southern dry forests
Juncus tenuis
Weeds typical of northern heavy soils
*Achillea millefolium**
*Chrysanthemum leucanthemum**
Oxalis europaea
*Phleum pratense**
*Plantago major**
Potentilla norvegica
Prunella vulgaris
*Trifolium repens**

An additional 111 species recorded in the Enterprise Radiation Forest outside site 1 are listed in Table 2. This number includes 9 shrubs; 5 ferns, horsetails, and club mosses; 12 grasses; 20 sedges and rushes; and 65 forbs. The nomenclature throughout follows Gleason (1968).

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*Species not native to North America. The majority of the abundant road species that are not typical of the immediately surrounding forest are not native species.

Description and Classification of Plant Communities in Site 1 and the Control Area

6

J. ZAVITKOVSKI
Institute of Forest Genetics, North Central Forest Experiment Station, Forest Service, U. S. Department of Agriculture, Rhinelander, Wisconsin

ABSTRACT

Nine forest and three logging-road plant communities were sampled in the Enterprise Radiation Forest in northern Wisconsin. These communities were quantitatively described by simple ecological indicators—frequency, density, and basal area or cover—and were classified by comparing them to standard cover types of three classification systems. Three forest communities were similar to the aspen cover type, three others to the aspen–paper birch cover type, and one each to the paper birch and sugar maple–basswood cover types. One community was transitional. Seven of the nine communities were in early and two in more-advanced successional stages. Paper birch, red and sugar maple, and quaking aspen headed the list of important species, followed by beaked hazel, Carex pensylvanica, *and large-leaved aster. Among the top 23 species were 11 trees, 2 shrubs, and 10 herbs. The future composition of the nine stands is predicted on the basis of the relative representation of young tree, sapling, and tree-seedling species. The logging-road vegetation was not classified, but floristically it resembled old-field vegetation.*

The main objective of the study was to describe several natural forest communities in the Enterprise Radiation Forest in northern Wisconsin to provide a basis for assessing their compositional and structural changes after they have been gamma irradiated. Three forest types, tentatively classified as aspen, birch, and northern hardwood, were selected in two areas, site 1 and control area, and were sampled annually from 1969 to 1971. Forest communities of these types are very common in northern Wisconsin. They usually develop after logging and are perpetuated by present logging practices, which favor species with a high vegetative-regeneration potential (e.g., aspen, maple, basswood, and oak), and light-seeded species, such as paper birch. Conifers are typically absent or are of low frequency in the main canopy, but some (e.g., balsam fir and hemlock) may be more abundant in the lower strata.

Northern forests in Wisconsin have been studied extensively by J. T. Curtis and his coworkers from the University of Wisconsin. On the basis of these studies, Curtis (1959) ordinated the northern forest communities into a vegetational continuum and, for convenience, divided it into six broad segments: lowland wet, lowland wet–mesic, mesic, upland dry–mesic, upland dry, and boreal forests. All these names have strong connotations of both topography and soil-moisture regime. The studies showed that sugar maple was best adapted to mesic sites and dominated many mesic stands and that jack pine and tamarack had the same role on dry and wet sites, respectively. Although an average composition for each of the six forest types was presented, it is very difficult to classify and place a new stand into the continuum using its composition alone. It can be done, however, by following Curtis's procedure, which was based on importance values and adaptation indices of the trees composing the communities and largely ignored other strata.

Ohmann and Ream (1971) included frequencies of all vegetational components (trees, shrubs, herbs, and lower plants) in their ordination of the upland forest communities of the Boundary Waters Canoe Area in northern Minnesota. Using agglomerative clustering and principal-component analyses, they distinguished 12 plant communities and named 10 of them for the dominant tree species. Two of these communities, aspen–birch and maple–aspen–birch, were dominated by hardwoods.

A classification system for North American forests based on the present composition of the tree canopy was developed by a committee of the Society of American Foresters (SAF) (1954). Two forest regions (boreal and northern forests) and, within these, four cover types (aspen–paper birch, aspen, paper birch, and sugar maple–basswood) are pertinent to our study. The requirement that the species for which the type is named account for at least 50% of the dominant and codominant stems makes it easy to classify a new stand, but in many instances no equivalent can be found for the transitional stands.

STUDY AREA AND SAMPLING METHODS

The area for the first radiation study, site 1, was subjectively selected to include aspen, birch, and northern hardwood cover types. The center of this area was located on a logging road. The area had signs of past disturbance by logging and lacked homogeneity within the individual vegetational types but was reasonably flat within the effective radiation range (about 50 m from the center), and its well-developed tree, shrub, and ground-vegetation strata provided suitable conditions for a radiation study. The area is described in more detail elsewhere in this volume.

A preliminary survey indicated that quaking aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), red maple (*Acer rubrum*), and sugar maple

Table 1

LAYOUT OF SAMPLE PLOTS

Forest type	Transect code	Number of sample plots and subplots: 0.5 by 0.5 m, 5–10 m	1 by 1 m, 5–50 m	1 by 1 m, 50–150 m	Total number of plots
		Site 1			
Aspen	T1	20	29	20	49
	T2	*	18*	20	38
Birch	T1	*	18*	18†	36
	T2	20	29	20	49
Northern hardwood	T1	20	29	20	49
	T2	20	29	20	49
Road	T	40	30	20	50
		Control Area			
Aspen	C				20
Birch	C				20
Northern hardwood	C				20
Road	C				20

*Sample plots located within the first 14 m from the center were added to the road transect.
†Two plots located in a swamp 150 m distant were not sampled.

(*A. saccharum*) were the most common and important tree species in site 1. Several other broad-leaved tree species and one gymnosperm, balsam fir (*Abies balsamea*), were also present in numbers sufficient for meaningful experimentation. The shrub layer was dominated by beaked hazel (*Corylus cornuta*), and a sedge (*Carex pensylvanica*), large-leaved aster (*Aster macrophyllus*), bracken fern (*Pteridium aquilinum*), wild sarsaparilla (*Aralia nudicaulis*), and mountain rice (*Oryzopsis asperifolia*) were prominent in the ground layer.

A control area with the same cover types was selected about 400 m from site 1. The composition of the tree and ground-vegetation layers was similar to the corresponding cover types of site 1, but the shrub layer was practically absent in the birch and northern hardwood forest types of the control area.

Boundaries of the three subjectively selected forest types in site 1 were delineated, and in each two transects were laid out at random from the center to 150 m. One additional transect, which featured a different, mostly introduced, herbaceous flora, was established on the logging road.

Each cover type was divided into two parts, one within the expected effective radiation range (from the center out to 50 m) and the other outside that range. The communities in each part were sampled and described separately. As a result eight summaries for site 1 (two for each cover type, including the road) and four summaries for the control area are presented.

For sampling purposes the vegetation was divided into four classes:

Trees. Woody species larger than 2.5 cm in diameter at breast height (dbh).

Tall shrubs. Woody species taller than 1 m but smaller than 2.5 cm in dbh.

Low shrubs. Woody species between 30 and 100 cm in height.

Ground vegetation. All herbaceous species, and woody species less than 30 cm in height.

In analyzing the data, I pooled tall and low shrubs into one class of shrubs.

All trees within 50 m of the center of site 1 were numbered, and their distance and elevation in relation to the center was determined with a transit. Between 50 and 150 m in site 1 and in the control area, all trees within 10-m-wide strips established along each transect were numbered and mapped. Details are presented elsewhere in this volume. The information recorded included a count by species and diameter at breast height. The average age of trees in the 50-m area was determined from increment cores extracted from a 10% sample.

Shrubs were sampled in paired 2- by 1-m (low shrubs) and 2- by 2-m (tall shrubs) sample plots located at 5-m intervals between 5 and 50 m, and at 10-m intervals between 50 and 150 m from the centers of site 1 and the control area. A total of 40 plots for each class of shrubs was established along each of the six transects in site 1, and 20 plots were established along each of the three control transects. Low and tall shrubs were counted and recorded by species for each sample plot. In 1971 the cover contributed by each species was subjectively estimated.

To sample ground vegetation, I staked out 49 1- by 1-m sample plots along each transect in site 1. These 1- by 1-m sample plots were subdivided into four 0.5- by 0.5-m subplots between 5 and 10 m from the center, and the ground vegetation was sampled separately within each plot and subplot. Only data on 1- by 1-m plots are presented here, however. Sample plots located within the first 14 m of one of the aspen and one of the birch transects intersecting the logging road were added to the road transect. Paired 1- by 1-m sample plots were established 10 m apart in each of the control transects. A detailed layout of the sample plots is given in Table 1. The species present in each sample plot were listed and frequencies were calculated. In 1971 cover percentages of individual species and total vegetation were subjectively estimated for each sample plot. The sampling was initiated in late summer of 1969 and updated in 1970 and 1971 to determine changes resulting from ingrowth and mortality.

Simple ecological indicators (frequency, density, and basal area or cover) and a combination of their relative values into one importance value (IV) (Curtis and McIntosh, 1951) were used to quantify and evaluate the importance of the component species of the sampled communities. The degree of similarity among the nine forest and three logging-road communities was evaluated by coefficients of community (CC), all based on Jaccard's index of similarity. The CC was calculated from absolute values of frequency, density, and basal area or cover separately for the tree, shrub, and ground-vegetation layers using the general formula

$$CC = \frac{2w}{a + b} 100$$

where a and b are sums of the quantitative values in the first and second communities and w is the sum of the smaller values of species common to both communities (Oosting, 1956; Curtis, 1959;

Douglas and Ballard, 1971). These coefficients range from 0 to 100.

On the basis of the w value of the coefficient of community calculated from basal areas of trees, the nine forest communities were ordinated in two dimensions, along x and y axes. Reference communities representing vegetational extremes were chosen on the basis of least similarity (i.e., smallest w value), and the remaining communities were arranged along the axes by the formula of Bray (1955)

$$X \text{ (or } Y) = \frac{Iw + CRw}{2}$$

where X (or Y) = position of a given stand on the gradient

Iw = w value of the given stand with reference stand 2

CRw = largest w value of the set of w values minus Rw

Rw = w value of the given stand with reference stand 1

The floristic richness of the sampled communities was evaluated by the average number of species per sample plot and by the Shannon–Weaver index of diversity (ID), estimated as $-\Sigma\, p_i \log_2 p_i$ (Shannon, 1948), where p_i is the fraction of total plant cover contributed by the *ith* species of a community. Cover values of rare species were arbitrarily set at 0.1%. Higher values of this index indicate greater diversity and floristic richness. The equitability component of the diversity (the evenness of distribution of individuals among species) was calculated by the formula

$$J = \frac{ID}{\log_2 s}$$

where ID is the Shannon–Weaver index of diversity and s is the number of species composing the community (Pielou, 1969).

The nomenclature of herbs and shrubs follows *Gray's Manual of Botany* (Fernald, 1950), and that of trees follows Little (1953).

The number of tables in this chapter may be found excessive by the average reader. They are included to aid outside cooperators who do not have direct access to the original data. Additional summaries, including data on individual sample plots, statistical tests, etc., are available on request.

DESCRIPTION OF COMMUNITIES

Results are presented separately for site 1, within and outside the effective radiation range, and for the control area. Nine forest communities are described quantitatively, and their mutual relationship is evaluated by coefficients of community calculated from frequency, density, and basal area or cover. Finally, these nine communities are ordinated as explained previously. The three logging-road communities are treated in a similar way except for ordination. Average values of ground vegetation data presented in the text are means of two transects, T1 and T2. Total numbers of ground-vegetation species include species found in both transects. In the tables data for T1 and T2 are listed separately.

Site 1

Area Within 50 m of the Site Center The communities within the area from the site center out to 50 m (7854 m^2) were sampled more intensively because they will be strongly affected by the radiation treatment. This area is almost level, sloping gently toward the north. Soil-moisture conditions were generally favorable except for two small areas where moisture was excessive during the major part of the growing season.

The three vegetation strata, trees, shrubs, and ground layer, were well developed and were generally similar in all three cover types. The trees were uniformly spaced, but in several places the crown cover was incomplete (estimated at 85%) because of small openings above the logging road and the two wet areas mentioned.

The average age of trees was 24.4 years, with a standard deviation of 10.4 years and a coefficient of variation of 42.6%. More-detailed information on age distribution is presented in Chap. 7, this volume.

Aspen Forest Type (A1) The area of 1506 m^2 occupied by the aspen forest type had a total of 428 trees (corresponding to 2842 trees per hectare) of 15 species. Quaking aspen accounted for more than half of all individuals and of the total basal area (Table 2); red maple and paper birch were also abundant. In comparison to most other sampled stands, the total basal area (17.99 m^2/ha) was low. Quaking aspen occurred here as an almost mature tree and in thickets of young saplings. Paper birch trees were mostly large, and red maples were small.

Fifteen low and tall shrub species were identified in this area (Table 3); the average was 1.70 low and 1.06 tall shrub species per 2- and 4-m^2 plots, respectively (Table 4). The average shrub density (5.89 per square meter) and the cover (24.7%) were the highest among all communities sampled. Densities remained very stable over a period of three years, with 6.01, 6.15, and 5.89 shrubs per square meter for 1969, 1970, and 1971, respectively (Table 5). Beaked hazel was the most important shrub species, accounting for about one-third of all frequencies, two-thirds of the total density, and 85% of the cover (Table 3). Other important shrubs were sow-teat blackberry (*Rubus allegheniensis*), velvet-leaf blueberry (*Vaccinium myrtilloides*), juneberry (*Amelanchier* sp.), and northern bush honeysuckle (*Diervilla lonicera*).

The ground vegetation was diverse, with an average of 16.3 species per square meter plot (Table 6). (This and subsequent averages are mean values of two transects.) Of a total of 85 species identified in this layer in 1970, 66 were herbaceous and 19 woody (Table 7). Seven herbaceous species [*Carex pensylvanica*, mountain rice, large-leaved aster, bunchberry (*Cornus canadensis*), bracken fern, wood anemone (*Anemone quinquefolia*), and common strawberry (*Fragaria virginiana*)] and two woody species (northern bush honeysuckle and beaked hazel) had average frequencies higher than 50% (Table 7). Bracken fern, sedge, large-leaved aster, wild sarsaparilla, and beaked hazel each covered more than 3% of the ground (Table 8). The total ground-vegetation cover averaged 93.5%, to which bracken fern contributed about one-third.

Birch Forest Type (B1) The birch forest type covered 2640 m^2 with a total of 550 trees (a density of 2080 trees per hectare) of 16 species (Table 2). Quaking aspen, red maple, and paper birch were the three most important species, accounting jointly for more than 70% of all individuals and of the total basal area. The total basal area (16.54 m^2/ha) was the lowest of all nine forest stands sampled. As in the aspen forest type, quaking aspen occurred both as mature trees and

Table 2

FREQUENCY (F),* DENSITY (D), AND BASAL AREA (BA) OF TREES IN THREE FOREST TYPES WITHIN 50 m OF CENTER IN SITE 1

Species	Aspen (A1)			Birch (B1)			N. hardwood (NH1)		
	F, %	D, no./ha	BA, dm²/ha	F, %	D, no./ha	BA, dm²/ha	F, %	D, no./ha	BA, dm²/ha
Abies balsamea	15	20	73	18	30	30	11	8	26
Acer rubrum	75	477	236	85	530	355	85	534	487
Acer saccharum	30	73	51	58	182	99	48	200	212
Amelanchier sp.	15	86	16	15	26	7	11	27	13
Betula alleghaniensis				3	11	3	24	62	15
B. papyrifera	35	106	193	67	227	283	67	189	330
Fraxinus nigra	15	40	20	21	99	55	50	254	169
Ostrya virginiana	15	27	11	27	87	40	26	62	40
Populus grandidentata	5	45	14				4	1	9
P. tremuloides	100	1725	948	76	647	544	52	280	217
Prunus pensylvanica				9	12	5	17	35	4
Prunus serotina	35	113	97	33	83	118	17	40	109
Quercus rubra	20	27	122	12	19	101	17	19	62
Salix sp.	40	66	9	33	99	7	4	5	2
Tilia americana	5	7	1	6	15	7	26	113	122
Ulmus americana							6	32	48
Other species	15	30	8	6	13	<1	15	7	10
Total	420	2842	1799	469	2080	1654	480	1868	1875

*Frequencies were determined from plots 76 to 78 m² in size marked out in the aspen, birch, and northern hardwood forest types.

as saplings; paper birch was mostly mature, and red maple was small. In general, the tree layer of this stand was similar to the aspen stand and to the northern hardwood type described in the following section.

Nineteen low and tall shrub species were present in this area (Table 9); the average was 1.88 low and 1.12 tall shrub species per 2- and 4-m² sample plot, respectively (Table 4). The average shrub density (4.08 per square meter) was intermediate between the aspen and northern hardwood types and was stable from one year to the next, as illustrated by average densities of 4.46, 4.16, and 4.08 per square meter in 1969, 1970, and 1971, respectively (Table 5). Beaked hazel dominated this layer, having an average density of 2.24 shrubs per square meter and a cover of 11.0%, about 78% of the total (Table 9). Sow-teat blackberry, velvet-leaf blueberry, and juneberry were also important.

The diversity of the ground vegetation (16.8 species per square meter plot) was slightly higher than in the aspen cover type (Table 6). Of the 77 species identified in this type, 58 were herbaceous and 19 woody (Table 10). Frequencies of more than 50% were determined for *C. pensylvanica*, mountain rice,

Table 3

FREQUENCY, DENSITY, AND COVER OF LOW AND TALL SHRUBS IN ASPEN FOREST TYPE*

Species	Frequency, %					
	Low		Tall		Low and tall	
	0–50 m	50–150 m	0–50 m	50–150 m	0–50 m	50–150 m
Corylus cornuta	51.1	27.5	64.3	32.5	69.5	37.5
Vaccinium myrtilloides	8.6	52.5			8.6	52.5
Amelanchier sp.	15.0	26.5	13.5	27.5	16.0	30.0
Rubus allegheniensis	36.1	17.5	7.2		39.1	17.5
Acer rubrum	2.5	15.0	2.5	15.0	2.5	17.5
Abies balsamea		10.0		17.5		17.5
Populus tremuloides		5.0	5.0	2.5	5.0	7.5
Ilex verticillata	2.5	15.0		10.0	2.5	17.5
Prunus serotina	12.5	12.5	5.0	5.0	12.5	12.5
Alnus rugosa		5.0		15.0		17.5
Salix sp.	7.5	12.5		2.5	7.5	12.5
Betula papyrifera		2.5		7.5		7.5
Diervilla lonicera	22.6	2.5			22.6	2.5
Ledum groenlandicum		7.5				7.5
Kalmia polifolia		2.5				2.5
Quercus rubra	2.5	10.0		5.0	2.5	12.5
Tilia americana				2.5		2.5
Prunus virginiana	6.0		7.5		10.5	
Other species	7.1	10.0		2.5	7.1	10.0
Total	174.0	234.0	105.0	145.0	205.9	285.0
Number of species	14	20	7	13	15	22

*Data are taken from 1971 survey in site 1.

Table 3 (Continued)

Species	Density, no./m²					
	Low		Tall		Low and tall	
	0–50 m	50–150 m	0–50 m	50-150 m	0–50 m	50–150 m
Corylus cornuta	1.96	0.36	1.83	0.37	3.79	0.73
Vaccinium myrtilloides	0.22	1.91			0.22	1.91
Amelanchier sp.	0.16	0.34	0.03	0.14	0.19	0.48
Rubus allegheniensis	0.97	0.14	0.09		1.06	0.14
Acer rubrum	0.02	0.10	0.01	0.05	0.03	0.15
Abies balsamea		0.06		0.05		0.11
Populus tremuloides		0.04	0.01	0.03	0.01	0.07
Ilex verticillata	0.02	0.19		0.19	0.02	0.38
Prunus serotina	0.09	0.07	0.01	0.01	0.10	0.08
Alnus rugosa		0.06		0.12		0.18
Salix sp.	0.12	0.44		<0.01	0.12	0.44
Betula papyrifera		0.04		0.02		0.06
Diervilla lonicera	0.16	0.01			0.16	0.01
Ledum groenlandicum		0.30				0.30
Kalmia polifolia		0.07				0.07
Quercus rubra	0.02	0.07		0.01	0.02	0.08
Tilia americana				<0.01		<0.01
Prunus virginiana	0.12		0.03		0.15	
Other species	0.02	0.16	<0.01	<0.01	0.02	0.16
Total	3.88	4.36	2.01	1.00	5.89	5.36
Number of species	14	20	7	13	15	22

Species	Cover, %					
	Low		Tall		Low and tall	
	0–50 m	50–150 m	0–50 m	50–150 m	0–50 m	50–150 m
Corylus cornuta	5.0	1.1	16.1	3.1	21.2	4.2
Vaccinium myrtilloides	0.2	2.2			0.2	2.2
Amelanchier sp.	0.2	0.9	0.3	0.8	0.5	1.7
Rubus allegheniensis	1.1	0.1	<0.1		1.2	0.1
Acer rubrum	<0.1	0.1	0.4	0.6	0.4	0.7
Abies balsamea		0.7		0.8		1.5
Populus tremuloides		<0.1	0.2	<0.1	0.2	0.1
Ilex verticillata	<0.1	0.1		<0.1	<0.1	0.2
Prunus serotina	0.2	0.1	0.3	<0.1	0.5	0.2
Alnus rugosa		0.2		1.5		1.7
Salix sp.	0.2	0.2		<0.1	0.2	0.2
Betula papyrifera		<0.1		0.4		0.5
Diervilla lonicera	0.2	<0.1			0.2	<0.1
Ledum groenlandicum		0.5				0.5
Kalmia polifolia		0.9				0.9
Quercus rubra	<0.1	0.3		0.1	<0.1	0.4
Tilia americana				0.2		0.2
Prunus virginiana	0.1		<0.1		0.1	
Other species	<0.1	0.4	<0.1	<0.1	<0.1	0.5
Total	7.3	8.0	17.4	7.8	24.7	15.8
Number of species	14	20	7	13	15	22

large-leaved aster, wood anemone, Canada mayflower (*Maianthemum canadense*), large-leaved violet (*Viola incognita*), tree club moss (*Lycopodium obscurum*), and beaked hazel (Table 10). Four herbaceous species (*C. pensylvanica*, large-leaved aster, bracken fern, and mountain rice) jointly covered 33.8% of the ground and accounted for about two-thirds of the total cover of 51.9% (Table 11).

Northern Hardwood Forest Type (NH 1) The northern hardwood forest type occupied the largest part of the 50-m circle, having an area of 3780 m² with a total of 693 trees (corresponding to 1868 trees per hectare) of 19 species (Table 2). Red maple was the most important species in both density and basal area, but several other species, including paper birch, quaking aspen, sugar maple, black ash (*Fraxinus nigra*), and American basswood (*Tilia americana*), also accounted for large proportions of the total density and basal area (Table 2). The total basal area (18.75 m²/ha) was higher than in either of the two cover types previously discussed. Several minor species [yellow birch (*Betula allegheniensis*), American elm (*Ulmus americana*), basswood, and ironwood (*Ostrya virginiana*)] formed a distinct lowland cover type that was too small to require a separate description, however.

Thirteen low and tall shrub species grew in the area (Table 12); the average was 1.10 low and 0.80 tall shrub species per sample plot (Table 4). The average density (2.02 per square meter) and cover (17.3%) were the lowest among the three cover types in the 50-m area (Table 12). The leading role of beaked hazel was more pronounced here than in the previous types. It accounted for about two-thirds of all individuals and covered 14.4% of the ground, corresponding to 83% of the total shrub cover (Table 12). Winterberry (*Ilex verticillata*) was the only other significant shrub species.

The diversity of the ground vegetation with an average of 13.6 species per square meter plot was lower than in the birch and aspen types (Table 6). A total of 72 species, 55 herbaceous and 17 woody, were present in the ground layer of this community (Table 13). Seven herbaceous species (*C. pensylvanica*, large-leaved aster, mountain rice, wild sarsaparilla, large-leaved violet, wood anemone, and tree club moss) and two woody species (beaked hazel and northern bush honeysuckle) had frequencies of more

Table 4

AVERAGE NUMBER OF SHRUB SPECIES PER PLOT IN 1971

Forest type and zone	Number of plots	Average number of species per plot: Low shrubs (2-m^2 plots)	Tall shrubs (4-m^2 plots)
Site 1			
Aspen			
0–50 m	34	1.70	1.06
50–150 m	40	2.50	1.45
Total	74		
Mean		2.13	1.27
Birch			
0–50 m	40	1.88	1.12
50–150 m	38	1.16	0.38
Total	78		
Mean		1.52	0.75
Northern hardwood			
0–50 m	40	1.10	0.80
50–150 m	40	0.62	0.22
Total	80		
Mean		0.86	0.51
Control Area			
Aspen	20	1.10	0.60
Birch	20	0.30	0.10
Northern hardwood	20	0.20	0.15

than 50% each (Table 13). *Carex pensylvanica,* large-leaved aster, wild sarsaparilla, bracken fern, and lady fern (*Athyrium filix-femina*) jointly covered 50.0% of the ground and accounted for about three-fourths of the total cover of 65.5% (Table 14).

Area 50 to 150 m from the Site Center The topography, soil-moisture conditions, and flora of the three cover types were very variable. The aspen type incorporated two small bogs and bordered on a large swamp; the northern hardwood type was located on an upland flat area; and part of the birch type included the driest and least productive sites of the entire area. Soil moisture of the aspen type was mostly favorable or excessive, but that of the birch and northern hardwood types was mostly droughty.

The vegetation of these communities was extensively sampled. The areas allocated for sampling of trees, tall and low shrubs, and ground vegetation, were, respectively, 10.0, 0.8, 0.4, and 0.2% of the total area of 6.27 ha. The age of these communities was about the same as within the 50-m area. The crown cover of the aspen type was estimated at 85%, and that of the birch and northern hardwood types was 100%.

Aspen Forest Type (A2) Eighteen tree species were found in the aspen cover type, which had an average density of 2620 trees and a total basal area of 19.04 m^2/ha (Table 15). Although quaking aspen was the most numerous species, it accounted for only 27% of all trees and 45% of the total basal area. Jointly with bigtooth aspen (*Populus grandidentata*), it accounted for 30% of all trees and 54% of the total basal area. Paper birch and red maple also had high densities and large basal areas. Speckled alder (*Alnus rugosa*) occurred frequently in this cover type, accounting for about 15% of all individuals, but its basal area was only 2.2% of the total.

Twenty-two tall and low shrub species were identified here; the average was 2.50 low and 1.45 tall shrub species per plot (Tables 3 and 4). The average density (5.36 shrubs per square meter) was one of the highest in the nine communities, and the average cover (15.8%) was also high (Table 3). Among individual species, velvet-leaf blueberry was most dense, followed by beaked hazel, juneberry, willow (*Salix* sp.), and winterberry. The cover of beaked hazel was the highest, followed by velvet-leaf blueberry, juneberry, speckled alder, and balsam fir (*A. balsamea*), each with a cover of more than 1%.

The ground vegetation was diverse, with 14.6 species per square meter plot (Table 6). Of the 72 species identified in this layer, 47 were herbaceous and 25 woody (Table 7). Nine herbaceous and one woody species had frequencies of 50% or more (Table 7). Bracken fern and wild sarsaparilla jointly accounted for more than half of the total ground-vegetation cover of 77.1% (Table 8). The cover of *C. pensylvanica* (2.3%) was strikingly low here in comparison to the aspen type within 50 m, where it reached 11.9%.

Birch Forest Type (B2) Five of the 12 tree species present in the birch cover type accounted for more than 90% of the total density and basal area (Table 15). In descending order they were red maple, paper birch, red oak (*Quercus rubra*), sugar maple, and quaking aspen. The total density (2585 trees per hectare) was comparable to and the total basal area (23.33 m^2/ha) was intermediate between the aspen and northern hardwood types (Table 15). Red maple occurred mostly as saplings, and paper birch was approaching maturity. The large size and importance of red oak in this cover type was indicated by its basal area of 6.81 m^2/ha, which corresponds to about 29% of the total.

There was a total of 12 low and tall shrub species in this cover type (Table 9), with an average of 1.16 low and 0.38 tall shrub species per sample plot (Table 4). Total density was 2.45 shrubs per square meter, almost half of which were beaked hazel. Sow-teat blackberry and juneberry were the two other most numerous species. Beaked hazel accounted for about 80% of the total cover of 9.5% (Table 9).

The ground vegetation was less diverse than in the previously described communities; the average was 10.2 species per square meter plot (Table 6). Of the total of 61 species identified in this cover type, 43 were herbaceous and 18 woody. Six herbaceous species had frequencies higher than 50% (Table 10). To the total cover of 30.0%, *C. pensylvanica* and large-leaved aster jointly contributed about half (Table 11).

Northern Hardwood Forest Type (NH2) The total tree density (2495 trees

Table 5

MEAN DENSITIES OF LOW AND TALL SHRUBS, 1969 TO 1971

Zone and forest type	No. of plots sampled	Low shrubs, no./m²			Tall shrubs, no./m²			Low and tall, no. /m²		
		1969	1970	1971	1969	1970	1971	1969	1970	1971
				Site 1						
0–150 m										
Aspen (A1, A2)	74	4.15	4.14	4.14	1.66	1.54	1.46	5.81	5.68	5.60
Birch (B1, B2)	78	2.52	2.58	2.46	0.84	0.77	0.82	3.36	3.35	3.28
Northern hardwood (NH1, NH2)	80	1.16	1.06	0.98	0.43	0.39	0.42	1.59	1.45	1.40
Total	232									
Mean		2.57	2.55	2.49	0.96	0.88	0.89	3.53	3.43	3.38
0–50 m										
Aspen (A1)	34	3.96	4.16	3.88	2.05	1.99	2.01	6.01	6.15	5.89
Birch (B1)	40	3.16	2.98	2.82	1.30	1.18	1.26	4.46	4.16	4.08
Northern hardwood (NH1)	40	1.38	1.34	1.34	0.72	0.65	0.68	2.10	1.99	2.02
Total	114									
Mean		2.78	2.76	2.62	1.32	1.24	1.28	4.10	4.00	3.90
50–100 m										
Aspen (A2)	20	5.50	5.58	6.40	1.46	1.40	1.14	6.96	6.98	7.54
Birch (B2)	20	1.10	1.12	1.42	0.22	0.28	0.31	1.32	1.40	1.73
Northern hardwood (NH2)	20	1.38	1.05	0.78	0.16	0.09	0.14	1.54	1.14	0.92
Total	60									
Mean		2.66	2.62	2.87	0.61	0.59	0.53	3.27	3.17	3.40
110–150 m										
Aspen (A2)	20	3.12	2.65	2.32	1.18	0.92	0.85	4.30	3.57	3.17
Birch (B2)	18	2.67	3.31	2.78	0.50	0.42	0.39	3.17	3.73	3.17
Northern hardwood (NH2)	20	0.55	0.52	0.45	0.14	0.19	0.18	0.69	0.71	0.63
Total	58									
Mean		2.09	1.84	1.82	0.31	0.40	0.48	2.70	2.14	2.29
				Control Area						
Aspen (CA)	20	1.58	1.55	1.77	1.24	0.85	0.97	2.82	2.40	2.74
Birch (CB)	20	0.20	0.20	0.20	0.06	0.05	0.04	0.26	0.25	0.24
Northern hardwood (CNH)	20	0.05	0.15	0.15	0.15	0.11	0.04	0.20	0.26	0.19
Total	60									
Mean		0.61	0.63	0.71	0.48	0.34	0.38	1.09	0.97	1.09

per hectare) and total basal area (25.71 m²/ha) of the northern hardwood forest type were about average for the nine forest communities (Table 15). Of the 13 tree species present in this type, sugar maple and paper birch accounted for more than half of the trees and of the total basal area. Four other species [American basswood, ironwood, white ash (*Fraxinus americana*), and red oak] were also important. Sugar maple occurred mostly as saplings, and birch was mostly large.

Only 10 low and tall shrub species were found in this community (Table 12); the average was 0.62 low and 0.22 tall species per plot (Table 4). The total density (0.78 per square meter) and the total cover (5.1%) were among the lowest of the nine communities (Table 12). Beaked hazel was the most important shrub, followed by shrub-size sugar maple and ironwood.

The diversity of the ground flora was low, 7.9 species per square meter (Table 6). Of the 43 species found in this community, 27 were herbaceous and 16 woody (Table 13). The most important herb, *C. pensylvanica,* had an average cover of 16.2%, more than half of the total cover of 30.0% (Table 14). *Carex pensylvanica* and four other herbaceous and one woody species had frequencies higher than 50% (Table 13).

Control Area

The topography and aspect of the three communities of the control area were variable and different from those of site 1. The birch forest type was located on a steep south-facing hill, and adjacent to it, but on an upland flat, was the northern hardwood community. Both apparently had unfavorable soil-moisture

Table 6

AVERAGE NUMBER OF GROUND-VEGETATION SPECIES PER PLOT,* 1970 SAMPLING

Forest type and transect	Zone: 5–50 m, Species per plot	Zone: 5–50 m, SD†	Zone: 50–150 m, Species per plot	Zone: 50–150 m, SD†	Control area, Species per plot	Control area, SD†
Aspen						
T1	14.7	5.6	13.8	4.0		
T2	17.9	5.1	15.4	3.6		
Mean T1 and T2	16.3		14.6		12.0	2.5
Birch						
T1	16.7	4.8	9.4	2.7		
T2	16.8	4.0	11.0	2.7		
Mean T1 and T2	16.8		10.2		7.0	1.3
Northern hardwood						
T1	12.9	2.6	8.6	2.7		
T2	14.3	2.5	7.2	3.1		
Mean T1 and T2	13.6		7.9		5.4	1.9
Road						
T	20.7	3.3	16.3	2.9		
C					17.0	2.9

*The size of the sample plot was 1 by 1 m.
†Standard deviation.

Table 7

FREQUENCIES (%) OF GROUND VEGETATION IN ASPEN FOREST TYPE, 1969 AND 1970

	T1				T2					
	5–50 m (29 plots)		50–150 m (20 plots)		16–50 m (18 plots)		50–150 m (20 plots)		C (20 plots)	
Species	1969	1970	1969	1970	1969	1970	1969	1970	1969	1970
Herbaceous Species										
Carex pensylvanica	72.4	72.4	40.0	35.0	88.8	88.8	75.0	80.0	90.0	100.0
Oryzopsis asperifolia	79.3	82.7	55.0	60.0	55.5	66.6	85.0	95.0	80.0	85.0
Cornus canadensis	82.7	82.7	55.0	55.0	61.1	66.6	95.0	100.0	10.0	10.0
Pteridium aquilinum	27.5	41.3	60.0	60.0	83.3	88.8	80.0	95.0	95.0	95.0
Aster macrophyllus	62.0	62.0	30.0	30.0	94.4	100.0	55.0	60.0	100.0	100.0
Anemone quinquefolia	?	41.4	?	45.0	?	100.0	?	25.0	?	85.0
Aralia nudicaulis	58.6	58.6	50.0	55.0	33.3	38.8	90.0	100.0	5.0	5.0
Maianthemum canadense	41.3	41.3	70.0	75.0	5.5	11.1	70.0	75.0	70.0	75.0
Viola incognita	31.0	37.9	55.0	55.0	61.1	61.1	45.0	45.0	20.0	35.0
Gaultheria procumbens	44.8	48.2	55.0	60.0	5.5	11.1	60.0	60.0	50.0	50.0
Lycopodium obscurum	55.1	55.1		5.0	27.7	27.7	40.0	45.0	35.0	35.0
Fragaria virginiana	31.0	31.0	10.0	10.0	72.2	72.2	25.0	25.0	5.0	5.0
Trientalis borealis	34.4	48.2	20.0	30.0	22.2	22.2	50.0	50.0		
Lycopodium clavatum	17.2	13.7	55.0	65.0			45.0	50.0		
Pyrola virens	37.9	31.0	5.0		16.6	16.6	20.0	10.0	35.0	45.0
Galium triflorum	13.7	17.2	10.0	10.0	50.0	50.0	15.0	10.0	5.0	
Clintonia borealis	6.8	6.8	10.0	10.0	5.5	5.5	40.0	40.0	60.0	65.0
Pyrola rotundifolia	20.6	27.5	20.0	15.0	38.8	61.1				
Hieracium sp.	10.3	13.7	5.0	15.0	38.8	44.4	15.0	10.0	5.0	15.0
Brachyelytrum erectum	13.7	13.7			44.4	50.0	10.0	10.0	5.0	5.0
Aster umbellatus	13.7	13.7	5.0	10.0	38.8	38.8		10.0	20.0	20.0
Luzula acuminata	27.5	27.5			22.2	55.5			30.0	45.0
Coptis groenlandica	3.4	3.4	35.0	40.0			50.0	55.0	15.0	15.0

Table 7 (Continued)

Species	T1 5–50 m (29 plots) 1969	T1 5–50 m (29 plots) 1970	T1 50-150 m (20 plots) 1969	T1 50-150 m (20 plots) 1970	T2 16-50 m (18 plots) 1969	T2 16-50 m (18 plots) 1970	T2 50–150 m (20 plots) 1969	T2 50–150 m (20 plots) 1970	C (20 plots) 1969	C (20 plots) 1970
Prenanthes sp.	10.3	17.2	5.0	5.0	16.6	27.7	5.0		15.0	20.0
Mitchella repens	13.7	13.7			11.1	27.7			35.0	35.0
Athyrium filix-femina					27.7	38.8	5.0	10.0	5.0	5.0
Aster ciliolatus	10.3	24.1		10.0	16.6	22.2				5.0
Streptopus roseus	17.2	17.2				5.5		15.0	20.0	20.0
Number of herbaceous species	56	54	46	46	48	49	31	29	37	37
Woody Species										
Shrubs										
Diervilla lonicera	44.8	44.8	10.0	10.0	55.5	66.6	30.0	30.0	45.0	50.0
Corylus cornuta	58.6	58.6	15.0	20.0	44.4	55.5	30.0	25.0	25.0	35.0
Rubus allegheniensis	27.5	27.5	25.0	30.0	72.2	66.6	60.0	65.0	5.0	5.0
Vaccinium myrtilloides	6.8	6.8	60.0	65.0	11.1	11.1	25.0	25.0	5.0	5.0
R. pubescens	13.7	17.2			27.7	27.7	5.0	5.0		
R. strigosus			10.0	10.0	38.8	44.4				
Ledum groenlandicum			20.0	20.0			5.0	5.0		
Number of shrub species	7	6	11	10	7	7	7	7	5	5
Trees										
Acer rubrum	55.1	58.6	70.0	75.0	16.6	11.1	80.0	55.0	20.0	25.0
Prunus serotina	34.4	37.9	25.0	35.0	16.6	22.2	40.0	45.0	40.0	20.0
Amelanchier sp.	13.7	51.7	10.0	30.0	5.5	5.5	15.0	40.0	5.0	10.0
Abies balsamea	27.5	17.2	25.0	20.0	22.2	22.2	30.0	35.0	5.0	5.0
Betula papyrifera	51.7	41.3	15.0		33.3	22.2	30.0	15.0	5.0	5.0
Populus tremuloides	3.4	3.4	10.0	20.0	33.3	27.7	10.0	15.0		
Quercus rubra	3.4	3.4	20.0	20.0	16.6	11.1	10.0	10.0	5.0	
Fraxinus americana		3.4			5.5	5.5	15.0	15.0	10.0	
Acer saccharum	13.7	17.2	5.0	5.0						
Salix sp.	13.7	13.7	10.0	10.0						
F. nigra	27.5	10.3			5.5	5.5				
Prunus virginiana		3.4		5.0		5.5	5.0			
Number of tree species	11	13	9	9	9	10	11	11	7	5
Total number of species	74	73	66	65	64	66	49	47	49	47

conditions. The aspen forest type was located on a flat, lowland area well supplied with moisture. It was more open (85% crown cover) than the other two communities, which had complete crown cover.

The age of quaking aspen, paper birch, red oak, and white ash was estimated between 30 and 40 years except for thickets of small aspen about 6 to 10 years old. Sugar maples in the northern hardwood forest type were mostly small and from 15 to 25 years old.

Aspen Forest Type (CA) Twelve tree species were found in the control aspen forest type. Quaking aspen, red maple, and paper birch were dominant, accounting for about two-thirds of all individuals. The average density (2390 trees per hectare) was about average for all nine forest communities, and the total basal area (19.20 m^2/ha) was below average (Table 16).

The shrub layer of this community was poorly developed in comparison to the two aspen communities in site 1. Only nine shrub species were present here (Table 17), as reflected in the low average, 1.10 low and 0.60 tall shrub species per plot (Table 4). Frequencies and densities were also low. Only beaked hazel had a frequency of more than 50%, and its density (2.01 shrubs per square meter) accounted for about 75% of all individuals (Table 17).

The species diversity of ground vegetation was also lower than that of the other two aspen communities (Table 6). The ground layer was dominated by

bracken fern, large-leaved aster, and *C. pensylvanica;* these three species had a joint cover of 135.6% or about 91% of the total cover of 149.3% (Table 8). The cover of the fourth most abundant herbaceous species, mountain rice, was only 2.0%. Among woody species, only northern bush honeysuckle reached a frequency of 50% (Table 7) and, jointly with other woody species, a cover of 3.3% (Table 8).

Birch Forest Type (CB) Only eight tree species were found in the birch community. It was dominated by paper birch, which accounted for more than half of all trees and of the total basal area (Table 16). The density (3150 trees per hectare) and the total basal area (25.98 m^2/ha) were lower only than those determined in the control northern hardwood type described in the following section. Red oak and red and sugar maple were also important in the tree stratum.

The shrub layer of this community had only three species. The average number of species per plot was only 0.30 and 0.10 for low and tall shrubs, respectively (Table 4), and the average density (0.24 shrubs per square meter) was the second lowest among the nine forest communities. This stratum was very stable, however, as illustrated by low and tall shrub densities of 0.26, 0.25, and 0.24 for 1969, 1970, and 1971, respectively (Table 5).

The diversity of the ground layer was low, 7.0 species per square meter (Table 6). Of the 19 species found in this layer, 13 were herbaceous and 6 woody (Table 10). In 1970 six herbaceous and one woody species had frequencies of 50% or higher (Table 10). Three of the herbaceous species (*C. pensylvanica,* large-leaved aster, and bracken fern) had a joint cover of 74.3% or almost 94% of the total cover of 78.3% (Table 11). The pooled cover of all woody species was less than 1%.

Northern Hardwood Forest Type (CNH) The northern hardwood forest community also had only eight tree species and was dominated by four, red oak, paper birch, sugar maple, and white ash (Table 16). This was the densest community, having an equivalent of 3490 trees and a total basal area of 29.07 m^2/ha. Red oak and paper birch were mostly large, and the most numerous species, sugar maple, was small.

Table 8

AVERAGE COVER (%) OF GROUND-VEGETATION SPECIES IN 1971 SAMPLING OF ASPEN FOREST TYPE

Species	All aspen transects	T1		T2		C
		5–50 m	50–150 m	5–50 m	50–150 m	
Pteridium aquilinum	37.2	18.5	26.8	41.6	39.2	60.0
Aster macrophyllus	17.8	6.9	2.5	25.4	5.2	48.8
Carex pensylvanica	11.0	11.7	1.0	12.0	3.6	26.8
Aralia nudicaulis	6.5	5.9	4.6	3.7	17.9	0.2
Oryzopsis asperifolia	2.1	4.2	1.6	1.0	1.8	2.0
Cornus canadensis	2.0	0.8	1.4	0.8	6.8	0.1
Osmunda cinnamomea	2.0		9.8			
Corylus cornuta	1.8	4.2	0.4	2.7	0.8	0.9
Rubus allegheniensis	1.6	0.2	1.2	5.3	1.1	0.1
Vaccinium myrtilloides	1.2	<0.1	3.8	0.3	1.4	0.3
Diervilla lonicera	1.1	1.0	<0.1	2.8	0.8	0.9
Athyrium filix-femina	1.1			4.9	0.2	0.4
Aster umbellatus	0.9	0.3		3.7	0.2	0.5
Onoclea sensibilis	0.9	4.5				
Clintonia borealis	0.9	0.1	0.6	0.3	1.6	1.8
Maianthemum canadense	0.8	0.2	1.4		1.5	1.0
Gaultheria procumbens	0.6	0.6	1.6		0.5	0.4
Lycopodium obscurum	0.6	0.6			1.4	0.8
Carex sp. (other)	0.5		2.4			0.3
Carex arctata	0.5		1.8	0.7	0.1	<0.1
Scirpus cyperinus	0.5	2.6				
Hieracium sp.	0.5	0.1	0.2	2.1	0.1	<0.1
Prunus serotina	0.4	0.7	0.4		0.1	1.0
Luzula acuminata	0.4	0.5		0.3		1.3
Lycopodium clavatum	0.4	0.4	1.0		0.4	
Viola incognita	0.4	0.8	0.4	0.3	0.2	0.1
Fragaria virginiana	0.3	0.6		0.8	0.1	
Lycopus uniflorus	0.3		1.4			
Ledum groenlandicum	0.2		1.2			
Acer rubrum	0.2	0.4	0.6			<0.1
Subtotal, %	94.7	65.9	66.2	108.7	85.0	148.0
Total cover of all species, %	98.8	70.7	70.8	116.3	87.4	149.3
Total number of species	121	73	65	66	47	46

The low species diversity of the tree stratum was also present in both shrub and ground layers. Only four shrub species grew here, with only 0.20 low and 0.15 tall shrub species per 2- and 4-m^2 plots, respectively (Tables 4 and 17). The total density (0.18 shrubs per square meter) was the lowest in the nine communities.

Only 5.4 ground-layer species per square meter were determined for this community; this was reflected in the low total number of species, 25, of which 18 were herbaceous and 7 were woody (Tables 6 and 13).

Logging-Road Vegetation

The vegetation of the logging road was floristically very rich. Of a total of 91 species, 72 were herbaceous and 19 woody (Table 18). This richness was also shown in the average number of species per square meter plot, which was 20.7 within and 16.3 outside the 50-m boundary in site 1 and 17.0 in the control area (Table 6). That this vegetation was the most unstable among the communities sampled can be inferred from the changes in average numbers of species per square meter as well as from total numbers of

Table 9

FREQUENCY, DENSITY, AND COVER OF LOW AND TALL SHRUBS IN BIRCH FOREST TYPE*

Species	Frequency, %						Density, no./m²						Cover, %					
	Low		Tall		Low and tall		Low		Tall		Low and tall		Low		Tall		Low and tall	
	0–50 m	50–150 m	0–50 m	50–150 m	0–50 m	50–150 m	0–50 m	50–150 m	0–50 m	50–150 m	0–50 m	50–150 m	0–50 m	50–150 m	0–50 m	50–150 m	0–50 m	50–150 m
Corylus cornuta	65.0	23.0	65.0	20.6	75.0	26.2	1.15	0.82	1.09	0.30	2.24	1.12	3.8	3.4	7.2	4.2	11.0	7.6
Rubus allegheniensis	40.0	17.8	7.5	5.0	40.0	19.8	0.51	0.49	0.02	0.01	0.53	0.50	0.5	0.3	<0.1	<0.1	0.6	0.4
Amelanchier sp.	10.0	33.0	10.0	5.6	12.5	33.0	0.06	0.41	0.04	0.02	0.10	0.43	0.4	0.9	0.5	<0.1	0.9	0.9
Vaccinium myrtilloides	10.0	11.1	2.5		10.0	11.1	0.52	0.17	<0.01		0.53	0.17	0.4	0.2	<0.1		0.4	0.2
Populus tremuloides	12.5	5.0	7.5	2.5	15.0	5.0	0.13	0.08	0.02	<0.01	0.15	0.09	0.1	<0.1	0.1	<0.1	0.2	0.1
Acer saccharum	2.5	2.8	5.0		5.0	2.8	0.01	0.01	0.02		0.03	0.01	<0.1	<0.1	0.2		0.2	<0.1
Prunus serotina	7.5	5.2			7.5	5.2	0.05	0.02			0.05	0.02	0.2	<0.1			0.2	<0.1
Acer rubrum	7.5		5.0	2.8	10.0	2.8	0.05		0.01	<0.01	0.06	0.01	<0.1		0.1	0.1	0.1	0.1
Ilex verticillata		5.6	2.5		2.5	5.6		0.04	0.03		0.03	0.04		<0.1	0.2		0.2	<0.1
R. strigosus	7.5				7.5		0.11				0.11		0.1				0.1	
Salix sp.	5.0				5.0		0.05				0.05		0.1				0.1	
Tilia americana	2.5	2.5	2.5		2.5	2.5	0.09	0.02	0.01		0.10	0.02	<0.1	<0.1	<0.1		<0.1	<0.1
Diervilla lonicera	7.5				7.5		0.04				0.04		<0.1				<0.1	
Fraxinus sp.	2.5	5.0			2.5	5.0	0.01	0.03			0.01	0.03	<0.1	<0.1			<0.1	<0.1
Prunus virginiana	2.5		2.5		5.0		0.01		<0.01		0.02		<0.1		<0.1		<0.1	
Other species	5.0	2.7			5.0	2.7	0.03	0.01			0.03	0.01	<0.1	<0.1			<0.1	<0.1
Total	187.5	113.7	110.0	36.5	212.5	121.7	2.82	2.10	1.26	0.35	4.08	2.45	5.6	5.1	8.5	4.4	14.1	9.5
Total number of species	16	11	10	5	19	12	16	11	10	5	19	12	16	11	10	5	19	12

*Data are taken from 1971 survey in site 1.

Table 10

FREQUENCIES OF GROUND VEGETATION IN BIRCH FOREST TYPE, 1969 AND 1970

Species	T1				T2				C	
	16–50 m (18 plots)		50–140 m (18 plots)		5–50 m (29 plots)		50–150 m (20 plots)		C (20 plots)	
	1969	1970	1969	1970	1969	1970	1969	1970	1969	1970
Herbaceous Species										
Carex pensylvanica	94.4	100.0	55.5	61.1	93.1	100.0	100.0	100.0	100.0	100.0
Oryzopsis asperifolia	66.6	77.7	50.0	55.5	86.2	93.1	90.0	95.0	85.0	80.0
Aster macrophyllus	94.4	100.0	33.3	33.3	62.0	68.9	85.0	90.0	100.0	100.0
Maianthemum canadense	33.3	50.0	88.8	88.8	48.2	51.7	30.0	25.0	20.0	20.0
Gaultheria procumbens	27.7	27.7	72.2	72.2	68.9	68.9	30.0	30.0	60.0	60.0
Anemone quinquefolia	?	94.4	?		?	72.4	?	40.0	?	5.0
Viola incognita	72.2	77.7		5.5	41.3	51.7	55.0	55.0		
Lycopodium obscurum	72.2	66.6	11.1	11.1	41.3	48.2	45.0	45.0	15.0	10.0
Pteridium aquilinum			22.2	22.2	48.2	48.2	25.0	20.0	65.0	75.0
Aralia nudicaulis	16.6	11.1	61.1	61.1	34.4	37.9	40.0	40.0		
Cornus canadensis	27.7	16.6	44.4	27.7	72.4	72.4	25.0	15.0		
Trientalis borealis	16.6	33.3	44.4	44.4	37.9	41.3	5.0	5.0		
Hieracium sp.	27.7	22.2	5.5	5.5	34.4	55.1	40.0	40.0	15.0	10.0
Viola pubescens	33.3	44.4					15.0	20.0	35.0	50.0
Fragaria virginiana	11.1	11.1			55.1	51.7	30.0	25.0		
Prenanthes sp.	11.1	50.0	5.5	5.5	37.9	31.0	5.0			
Pyrola virens	38.8	38.8			37.9	34.4	20.0	10.0		
Pyrola rotundifolia	44.4	44.4			37.9	34.4	10.0	5.0		
Galium triflorum	27.7	33.3			17.2	31.0	20.0	10.0		

Table 10 (Continued)

Species	T1				T2				C	
	16–50 m (18 plots)		50–140 m (18 plots)		5–50 m (29 plots)		50–150 m (20 plots)		C (20 plots)	
	1969	1970	1969	1970	1969	1970	1969	1970	1969	1970
Luzula acuminata	33.3	44.4			3.4	13.7	5.0	15.0	10.0	10.0
Streptopus roseus	22.2	22.2			3.4	6.8	40.0	15.0	5.0	5.0
Aster ciliolatus	5.5	16.6			13.7	34.4	15.0	30.0		
Mitchella repens	27.7	27.7			13.7	17.2	15.0	15.0	5.0	5.0
Lycopodium clavatum	5.5	5.5	11.1	16.6	13.7	20.6				
Clintonia borealis	16.6	22.2	16.6	11.1	10.3	10.3		5.0		
Aster umbellatus	5.5	5.5			10.3	24.1	10.0	10.0		
Athyrium filix-femina	22.2	16.6			10.3	6.8	5.0	5.0		
Brachyelytrum erectum	33.3	33.3			10.3	10.3	15.0	20.0		
Number of herbaceous species	51	45	22	21	58	50	42	37	16	13
Woody Species										
Shrubs										
Corylus cornuta	72.2	72.2	22.2	16.6	31.0	41.3	45.0	35.0	15.0	15.0
Rubus allegheniensis	38.8	33.3	11.1	11.1	48.2	58.6	45.0	35.0		
Diervilla lonicera	27.7	27.7	11.1	11.1	41.3	44.8	40.0	30.0		
Vaccinium myrtilloides	5.5	5.5	22.2	27.7	37.9	37.9	5.0			
R. strigosus	27.7	27.7			24.1	24.1		5.0		

Table 10 (Continued)

Species	T1				T2				C	
	16–50 m (18 plots)		50–140 m (18 plots)		5–50 m (29 plots)		50–150 m (20 plots)		C (20 plots)	
	1969	1970	1969	1970	1969	1970	1969	1970	1969	1970
R. pubescens	11.1	11.1			27.5	27.5	10.0	5.0		
Number of shrub species	7	8	6	6	8	8	5	5	3	3
Trees										
Acer rubrum	44.4	33.3	77.7	50.0	62.0	55.1	20.0	30.0		
Amelanchier sp.	11.1	22.2	77.7	77.7	24.1	31.0	10.0	10.0	5.0	
Acer saccharum	50.0	38.8	22.2	11.1	27.5	37.9	50.0	35.0	10.0	10.0
Fraxinus americana	5.5	5.5	11.1	11.1	3.4	10.3	20.0	20.0	95.0	100.0
Prunus serotina	33.3	33.3	16.6	22.2	6.8	24.1		20.0	25.0	25.0
Quercus rubra	11.1	5.5	38.8	33.3	24.1	31.0	15.0	15.0	5.0	
Abies balsamea	22.2	16.6	44.4	44.4	20.6	17.2	5.0	5.0		
Betula papyrifera	16.6	22.2	33.3	44.4	24.1	13.7	5.0			
Populus tremuloides	11.1	27.7			3.4	6.8	20.0	15.0		
Prunus virginiana		5.5				3.4	5.0	5.0		
Salix sp.					6.8	10.3				
Number of tree species	10	10	8	8	11	11	10	9	6	3
Total number of all species	68	63	36	35	77	69	57	51	25	19

Table 11

AVERAGE COVER (%) OF GROUND-VEGETATION SPECIES IN 1971 SAMPLING OF BIRCH FOREST TYPE

Species	All birch transects	T1		T2		C
		5–50 m	50–150 m	5–50 m	50–150 m	
Carex pensylvanica	17.3	10.6	0.5	12.4	19.1	43.7
Aster macrophyllus	8.6	16.3	0.4	3.7	11.4	11.0
Pteridium aquilinum	7.2		2.8	11.4	2.0	19.6
Oryzopsis asperifolia	3.3	2.0	0.9	7.2	4.4	1.8
Aralia nudicaulis	1.9	0.4	2.5	4.1	2.6	
Rubus allegheniensis	1.0	1.3	0.2	2.2	1.3	
Viola incognita	0.9	2.9	<0.1	0.6	0.7	
Corylus cornuta	0.7	1.7	0.1	0.4	1.1	0.1
Vaccinium myrtilloides	0.7	0.2	0.3	2.9		
Viola pubescens	0.5	1.1			0.4	0.8
Maianthemum canadense	0.5	<0.1	0.7	0.6	0.4	0.1
Gaultheria procumbens	0.4		0.4	1.0	<0.1	0.5
Diervilla lonicera	0.4	0.3	0.4	0.6	0.5	
Onoclea sensibilis	0.3			1.7		
Aster ciliolatus	0.3	0.3	<0.1	0.7	0.6	
Hieracium sp.	0.3	0.3		0.7	0.6	<0.1
Cornus canadensis	0.3	<0.1	0.1	1.2	0.2	
Acer saccharum	0.3	0.8		0.5	0.1	0.1
Athyrium filix-femina	0.3	1.0			0.5	
Lycopodium obscurum	0.3	0.5	0.2	0.4	0.4	
Amelanchier sp.	0.3	0.3	0.9	0.1	<0.1	
Fragaria virginiana	0.3	<0.1		0.9	0.4	
Prenanthes sp.	0.3	0.8		0.5	<0.1	
Streptopus roseus	0.2	0.7		<0.1	0.4	
R. strigosus	0.2	0.6		0.4	0.1	
Clintonia borealis	0.2	0.3	<0.1	0.3	0.2	
Subtotal, %	47.0	42.6	10.8	54.6	47.4	77.8
Total cover of all species, %	48.4	45.2	11.3	58.6	48.8	78.3
Total number of species	95	63	35	69	51	19

Table 12

FREQUENCY, DENSITY, AND COVER OF LOW AND TALL SHRUBS IN NORTHERN HARDWOOD FOREST TYPE*

Species	Frequency, %						Density, no./m²						Cover, %					
	Low		Tall		Low and tall		Low		Tall		Low and tall		Low		Tall		Low and tall	
	0–50 m	50–150 m	0–50 m	50–150 m	0–50 m	50–150 m	0–50 m	50–150 m	0–50 m	50–150 m	0–50 m	50–150 m	0–50 m	50–150 m	0–50 m	50–150 m	0–50 m	50–150 m
Corylus cornuta	62.5	27.5	57.5	15.0	67.5	30.0	0.83	0.34	0.54	0.12	1.37	0.46	5.0	1.9	9.4	1.7	14.4	3.6
Ilex verticillata	2.5		5.0		5.0		0.18		0.09		0.27		0.5		0.9		1.4	
Fraxinus sp.	7.5	2.5	5.0		10.0	2.5	0.06	0.01	0.01		0.07	0.01	0.1	<0.1	0.7	<0.1	0.8	0.1
Ostrya virginiana		5.0		10.0		12.5		0.09		0.03		0.12		0.2		<0.1		0.2
Acer saccharum		7.5		2.5		7.5		0.05		<0.01		0.06		<0.1		1.0		1.0
Populus tremuloides	7.5	5.0			7.5	5.0	0.06	0.03			0.06	0.03	<0.1	<0.1			<0.1	<0.1
Prunus serotina	7.5		5.0		10.0		0.04		0.01		0.05		<0.1		0.1		0.1	
Acer rubrum	2.5		2.5		2.5		0.01		<0.01		0.02		<0.1		<0.1		0.1	
Amelanchier sp.	5.0		2.5		5.0		0.05		<0.01		0.06		<0.1		<0.1		0.1	
Betula papyrifera		5.0				5.0		0.08				0.08		<0.1				<0.1
Diervilla lonicera	5.0				5.0		0.04				0.04		<0.1				<0.1	
Cornus alternifolia	2.5	2.5	2.5		2.5	2.5	0.01	0.01	<0.01		0.02	0.01	<0.1	<0.1	<0.1		0.1	<0.1
Prunus virginiana	2.5				2.5		0.01				0.01		0.1				0.1	
Vaccinium myrtilloides	2.5				2.5		0.03				0.03		<0.1				<0.1	
Ribes sp.	2.5				2.5		0.02				0.02		<0.1				<0.1	
Other species		2.5				2.5		0.01				0.01		<0.1				<0.1
Total	110.0	57.5	80.0	27.5	122.5	67.5	1.34	0.62	0.68	0.16	2.02	0.78	6.1	2.3	11.2	2.8	17.3	5.1
Total number of species	12	8	7	4	13	10	12	8	7	4	13	10	12	8	7	4	13	10

*Data are taken from 1971 survey in site 1.

Table 13

FREQUENCIES (%) OF GROUND VEGETATION IN
NORTHERN HARDWOOD FOREST TYPE, 1969 AND 1970

	T1				T2					
	5–50 m (29 plots)		50–150 m (20 plots)		5–50 m (29 plots)		50–150 m (20 plots)		C (20 plots)	
Species	1969	1970	1969	1970	1969	1970	1969	1970	1969	1970
Herbaceous Species										
Carex pensylvanica	100.0	100.0	95.0	95.0	96.5	96.5	100.0	100.0	100.0	100.0
Aster macrophyllus	100.0	100.0	55.0	60.0	75.8	75.8	60.0	60.0	60.0	60.0
Oryzopsis asperifolia	75.8	82.7	75.0	85.0	55.1	62.0	30.0	30.0	60.0	75.0
Maianthemum canadense	34.4	27.5	60.0	60.0	37.9	34.4	75.0	80.0	55.0	55.0
Aralia nudicaulis	58.6	58.6	60.0	65.0	62.0	72.4	60.0	45.0	10.0	5.0
Viola incognita	72.4	79.3	10.0	10.0	58.6	72.4	60.0	60.0		
Anemone quinquefolia	?	62.1	?	15.0	?	68.8	?	50.0	?	20.0
Lycopodium obscurum	55.1	55.1	35.0	40.0	68.9	68.9	10.0	10.0	10.0	
V. pubescens	17.2	51.7	5.0	5.0	20.6	31.0	15.0	30.0	15.0	25.0
Trientalis borealis	13.7	24.1	15.0	15.0	44.8	44.8				
Mitchella repens	44.8	55.1	20.0	15.0	3.4	3.4	30.0	15.0		
Pteridium aquilinum		3.4	5.0	15.0	31.0	37.9			35.0	30.0
Luzula acuminata	6.8	27.5		5.0	31.0	44.8				
Cornus canadensis	24.1	24.1	10.0	5.0	41.3	41.3	10.0	5.0		
Pyrola virens	55.1	41.3	25.0	15.0	13.7	13.7	10.0	10.0		
Brachyelytrum erectum	17.2	17.2	15.0	15.0	31.0	27.5			10.0	10.0
Athyrium filix-femina	17.2	13.7	5.0	5.0	37.9	37.9			10.0	10.0
Clintonia borealis	6.8	6.8	20.0	20.0	24.1	31.0	5.0	10.0	5.0	5.0
Streptopus roseus	34.3	27.5	10.0	10.0	3.4	6.8	15.0	15.0	5.0	5.0
Trillium grandiflorum	10.3	13.7	20.0	20.0	6.8	10.3		5.0	10.0	10.0
Carex sp. (other)	3.4		10.0	10.0	34.4	34.4				
Pyrola rotundifolia	6.8	10.3					5.0	5.0		
Dryopteris spinulosa	6.8	6.8	10.0	20.0	24.1	24.1				
Gaultheria procumbens	17.2	17.2			10.3	13.7			15.0	10.0
Galium triflorum	17.2	13.7	5.0		27.5	20.6	5.0	5.0		
Aster umbellatus	13.7	17.2			13.7	13.7	5.0	5.0		
Uvularia sessilifolia	13.7	3.4	5.0	10.0			10.0	20.0		5.0
Prenanthes sp.	3.4	10.3			6.8	17.2	5.0	5.0		
Number of herbaceous species	38	37	24	24	48	46	23	24	21	18
Woody Species										
Shrubs										
Corylus cornuta	51.7	65.5	35.0	40.0	24.1	37.9	15.0	20.0	5.0	5.0
Diervilla lonicera	58.6	62.0	5.0	5.0	48.2	51.7	5.0			
Rubus pubescens	20.6	13.7	5.0	5.0	48.2	24.1				
Cornus alternifolia			10.0	10.0			15.0	15.0		
Vaccinium myrtilloides	3.4	6.8			6.8	6.8				
Number of shrub species	6	5	5	5	7	7	4	2	2	2
Trees										
Fraxinus americana	6.8	6.8	85.0	75.0	13.7	13.7	55.0	40.0	75.0	60.0
Prunus serotina	6.8	27.5	15.0	20.0	17.2	20.6	30.0	30.0	30.0	25.0
Acer saccharum	31.0	27.5	60.0	25.0	31.0	13.7	30.0	15.0		
Acer rubrum	27.5	27.5	20.0		37.9	27.5	5.0	5.0	5.0	5.0
Amelanchier sp.	31.0	37.9		10.0	10.3	13.7	10.0	10.0		
Betula papyrifera			20.0	20.0	6.8	6.8	10.0	10.0	10.0	15.0
Abies balsamea	17.2	27.5			6.8		5.0	5.0		
Populus tremuloides	10.3			10.0	20.6	20.6	5.0			

Table 13 (Continued)

Species	T1 5–50 m (29 plots) 1969	1970	T1 50–150 m (20 plots) 1969	1970	T2 5–50 m (29 plots) 1969	1970	T2 50–150 m (20 plots) 1969	1970	C (20 plots) 1969	1970
Quercus rubra	6.8	3.4	10.0	5.0	3.4	3.4	20.0	10.0	5.0	5.0
F. nigra					27.5	20.6	5.0	5.0		
Prunus virginiana	17.2	17.2				3.4				
Tilia americana			10.0	10.0				5.0		
Number of tree species	9	8	7	8	10	10	10	10	5	5
Total number of all species	53	50	36	37	65	63	37	36	28	25

Table 14

AVERAGE COVER (%) OF GROUND-VEGETATION SPECIES IN 1971 SAMPLING OF NORTHERN HARDWOOD FOREST TYPE

Species	All NH transects	T1 5–50 m	T1 50–150 m	T2 5–50 m	T2 50–150 m	C
Carex pensylvanica	17.5	14.3	18.9	12.1	13.5	28.8
Aster macrophyllus	7.9	20.6	0.7	13.5	1.8	2.9
Aralia nudicaulis	4.3	5.1	7.8	6.3	2.1	
Pteridium aquilinum	3.2		0.6	13.0		2.6
Athyrium filix-femina	3.1	4.8	0.1	10.3		0.2
Oryzopsis asperifolia	1.9	3.0	3.5	1.7	0.8	0.4
Viola pubescens	1.0	1.6	0.1	0.7	1.9	0.5
Maianthemum canadense	0.8	0.3	1.0	0.5	1.4	0.6
Corylus cornuta	0.7	2.1	0.8	0.6		
Lycopodium obscurum	0.5	0.8	0.5	0.9	0.1	
Lycopus uniflorus	0.4			2.0		
Clintonia borealis	0.3	0.1	0.4	1.0	0.1	
Rubus pubescens	0.3	<0.1		1.5		
Diervilla lonicera	0.3	0.5		0.8		
Streptopus roseus	0.3	0.4	0.2	0.4	0.1	0.2
Luzula acuminata	0.2	0.3		0.8		
Cornus alternifolia	0.2		0.8		0.2	
Iris versicolor	0.2			0.9		
Anemone quinquefolia	0.2	0.2	<0.1	0.3	0.2	0.1
Carex arctata	0.2	0.2		0.6		
Prenanthes sp.	0.2	0.2		0.6		
Trillium grandiflorum	0.2	<0.1	0.3	<0.1	<0.1	0.3
Subtotal, %	43.9	54.6	35.8	68.6	22.2	36.6
Total cover of all species, %	45.7	57.5	37.3	73.5	22.6	37.7
Total number of species	77	50	37	63	36	25

Table 15

FREQUENCY* (F), DENSITY (D), AND BASAL AREA (BA) OF TREES IN THREE FOREST TYPES 50 TO 150 m FROM CENTER OF SITE 1

Species	Aspen (A2)			Birch (B2)			N. hardwood (NH2)		
	F, %	D, no./ha	BA, dm^2/ha	F, %	D, no./ha	BA, dm^2/ha	F, %	D, no./ha	BA, dm^2/ha
Abies balsamea	46.2	70	77	15.4	25	31	3.9	5	<1
Picea mariana	15.4	55	32						
Acer rubrum	92.3	580	268	76.9	950	397	38.4	100	98
Acer saccharum	15.4	35	3	73.0	465	221	100.0	1325	784
Alnus rugosa	42.3	380	41						
Amelanchier sp.	7.7	20	2	23.1	70	17	3.9	5	2
Betula alleghaniensis	3.9	5	2	3.9	10	16	15.4	35	12
B. papyrifera	88.5	570	383	69.2	470	663	73.0	380	609
Fraxinus americana				3.9	5	12	23.1	90	258
Ostrya virginiana							69.2	250	135
Populus grandidentata	30.7	80	165						
Populus tremuloides	92.3	710	861	34.6	270	231	7.7	10	92
Prunus pensylvanica	23.1	55	10	7.7	15	6			
Prunus serotina	15.4	25	2	15.4	35	29	11.5	30	57
Quercus rubra				57.6	235	681	15.4	50	231
Tilia americana				15.4	35	29	80.8	210	293
Additional species	23.0	35	59				3.9	5	<1
Total	496.2	2620	1905	396.1	2585	2333	446.2	2495	2571
Total number of species	18	18	18	12	12	12	13	13	13

*Frequency figures are based on 26 plots 77 m^2 in size in each forest type.

Table 16

1970 FREQUENCY (F), DENSITY (D), AND BASAL AREA (BA) OF TREES IN CONTROL AREA

Species	Aspen (CA)			Birch (CB)			N. hardwood (CNH)		
	F, %	D, no./ha	BA, dm^2/ha	F, %	D, no./ha	BA, dm^2/ha	F, %	D, no./ha	BA, dm^2/ha
Abies balsamea	15	20	3						
Acer rubrum	100	630	220	54	330	83	77	240	59
Acer saccharum	23	30	6	92	530	102	100	1230	172
Alnus rugosa	8	50	6						
Amelanchier sp.	31	110	18						
Betula papyrifera	85	230	241	100	1870	1564	85	880	788
Fraxinus americana				38	90	132	77	240	302
Ostrya virginiana	15	20	5	8	10	2	31	120	16
Populus grandidentata	31	70	102	31	40	99	8	20	37
Populus tremuloides	100	1070	1137						
Prunus serotina	31	50	61						
Quercus rubra	46	90	89	54	240	596	100	690	1513
Salix sp.	15	20	32						
Tilia americana				23	40	20	38	70	21
Total	500	2390	1920	400	3150	2598	516	3490	2908

Table 17

FREQUENCY (F) AND DENSITY (D) OF LOW AND TALL SHRUBS IN CONTROL AREA

	Aspen (CA)						Birch (CB)						N. hardwood (CNH)					
	F, %			D, no./m²			F, %			D, no./m²			F, %			D, no./m²		
Species	Low	Tall	L + T	Low	Tall	L + T	Low	Tall	L + T	Low	Tall	L + T	Low	Tall	L + T	Low	Tall	L + T
Acer rubrum	10	5	15	0.05	0.04	0.09												
Acer saccharum													5	15	20	0.02	0.04	0.06
Amelanchier sp.	5		5	0.02		0.02												
Betula papyrifera	5		5	0.08		0.08	10		10	0.05		0.05	10		10	0.05		0.05
Corylus cornuta	45	50	55	1.10	0.91	2.01	15	10	20	0.13	0.04	0.17	5		5	0.02		0.02
Diervilla lonicera	15		15	0.20		0.20												
Dirca palustris													5		5	0.05		0.05
Populus tremuloides	10		10	0.05		0.05	5		5	0.02		0.02						
Prunus serotina	10	5	15	0.05	0.02	0.07												
Tilia americana	5		5	0.02		0.02												
Vaccinium myrtilloides	5		5	0.20		0.20												
Total	110	60	130	1.77	0.97	2.74	30	10	35	0.20	0.04	0.24	25	15	40	0.14	0.04	0.18

species found between 1969 and 1971 (Table 18). The pronounced increase in numbers in site 1 in 1971 was caused primarily by new species that became established in some plots that previously had incomplete cover and also by small or solitary individuals that were overlooked in the 1969 and 1970 samplings.

Floristically this vegetation resembled old-field vegetation. Included were many species commonly called weeds, many of which had been introduced from other continents. Among the 33 species listed in Table 19, 9 were introduced from Europe, and the distribution of several others is transcontinental. Since many of them have light, wind-borne seeds or seeds eaten by birds and small rodents, they are widely dispersed. Also horse logging in this area, with attendant hay feeding, may have been influential here.

The logging-road communities had no single species that could be called dominant. "Dominance" was shared by many species, of which only common strawberry (*F. virginiana*) and large-leaved violet had an average cover higher than 5%. The cover of the next 16 important species ranged from 1 to 5% (Table 19). These 18 species, with a joint cover of 47.2%, accounted for about three-fourths of the total cover of 61.9%.

Table 18

FLORISTIC RICHNESS OF THE LOGGING-ROAD VEGETATION

Location, zone, and code	Total number of species								
	1969			1970			1971		
	Herb	Woody	All	Herb	Woody	All	Herb	Woody	All
Site 1									
0–50 m (R1)	51	12	63	54	13	67	57	13	70
50–150 m (R2)	38	11	49	36	11	47	41	12	53
0–150 m (R1, R2)	56	13	69	57	15	72	65	16	81
Control area (CR)	39	8	47	42	6	48	44	6	50
Both areas (R1, R2, CR)	64	15	79	66	17	83	72	19	91

Location, zone, and code	Number of plots	Average number of species per square meter plot		
		1969	1970	1971
Site 1				
0–50 m (R1)	30	18.7	20.7	23.4
50–150 m (R2)	20	12.8	16.3	18.9
Control area (CR)	20	15.8	17.0	17.1

Comparison of the Sample Communities

The relation among the nine forest stands was evaluated by coefficients of community (CC) calculated from frequency, density, and basal area or cover data of all three vegetation components—trees, shrubs, and ground vegetation (Table 20). Several comparisons were of special interest, including those among the three stands within the effective radiation range and among stands of the same forest types used in the initial classification.

The CC's among all three stands within the 50-m radius in site 1 were high, ranging from an average of 62 between the aspen and northern hard-

Table 19

1971 FREQUENCY (F) AND COVER (C) OF LOGGING-ROAD VEGETATION

	Site 1				Control area (CR)	
	0–50 m (R1)		50–150 m (R2)			
Species	F, %	C, %	F, %	C, %	F, %	C, %
Fragaria virginiana	100	8.0	100	5.8	90	8.1
Trifolium repens	89	5.7	100	3.8	85	1.0
*Rubus strigosus**	74	1.9	55	3.3	70	7.5
Viola incognita	100	11.1	35	0.5	55	8.2
Plantago major	89	2.2	95	1.0	100	2.4
Juncus tenuis	89	5.6	70	1.0	65	3.2
Solidago sp.	68	2.8	80	2.2	55	2.0
Erigeron annuus	53	2.2	65	1.3	65	2.6
Agrostis sp.	89	1.6	95	1.9	35	1.1
Aster umbellatus	79	6.4	95	3.4	25	0.6
Carex sp. (other)	68	0.8	80	1.0	55	2.8
Chrysanthemum leucanthemum	84	1.5	95	1.0	65	0.8
Achillea millefolium	79	2.4	75	1.2	40	0.6
Hieracium sp.	74	4.5	85	3.4	30	0.2
Aster ciliolatus	47	0.7	55	1.0	50	0.9
*Betula papyrifera**	47	1.0	80	2.0		
Prunella vulgaris	32	1.2	25	0.8	25	0.6
Geum virginianum	26	0.8	5	<0.1	70	5.0
Cornus canadensis	32	0.7	60	2.4		
Aster macrophyllus	42	2.0	30	0.5		
Potentilla norvegica	63	0.5	25	0.3	45	0.3
Galium triflorum	32	0.6			60	1.4
Gramineae (other)	11	0.1	15	0.7	35	1.2
Oxalis europaea	47	0.6			50	0.8
Athyrium filix-femina	21	0.1			45	4.4
Phleum pratense	47	0.6	40	0.4	5	<0.1
Galeopsis tetrahit					45	2.8
Epilobium glandulosum	42	0.2			65	1.8
Lycopus uniflorus	5	<0.1	10	0.1	15	2.6
Lychnis alba					55	0.8
Carex pensylvanica	32	1.0				
*Acer rubrum**	74	0.2	30	0.1		
Salix sp.*	53	0.6	55	1.2		
Other species		3.5		3.0		7.4
Total		71.1		43.3		71.3
Total number of species		70		53		50

*Woody species.

wood types to 71 between the aspen and birch types. These high values suggest that the entire area is located in transitional zones between the three forest types into which site 1 was initially divided. Measured by the CC, the different forest types (i.e., A1, B1, and NH1) within the 50-m radius were more similar to each other than were the three communities within the aspen (A1, A2, CA), birch (B1, B2, CB), or northern hardwood (NH1, NH2, CNH) types. The reason for this can be attributed to the shrub layer, which was well developed throughout the 50-m circle but was practically missing or poorly developed in the other six forest communities.

Based on CC values, the three stands originally called aspen (A1, A2, CA) type were more similar among themselves than the three stands initially called birch (B1, B2, CB) or northern hardwood (NH1, NH2, CNH). The average CC's for successive comparisons of communities within

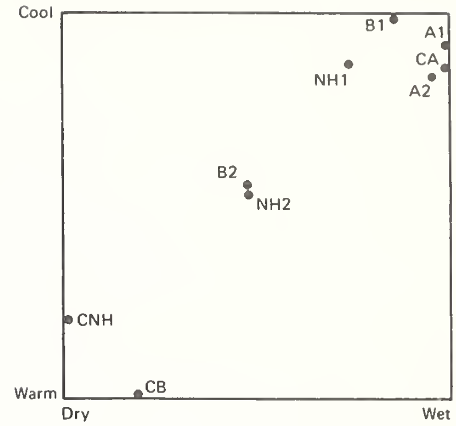

Fig. 1 Two-dimensional ordination of nine forest communities.

50 m, outside 50 m, and control were 59, 65, and 52, respectively, for aspen; 65, 31, and 41, respectively, for birch; and 48, 28, and 52, respectively, for northern hardwood (Table 20).

A two-dimensional ordination of the nine forest communities based on basal area of trees separated them into three dissimilar groups (Fig. 1). The two axes apparently represent moisture and temperature gradients. Five stands, the three within the 50-m area (A1, B1, NH1) and two aspen stands outside that area (A2, CA), cluster in one corner; two stands (CB, CNH) separate in the opposite corner, and two stands (B2, NH2) appear in the center of the diagram. Although no quantitative evidence is available at this time to support this ordination, a subjective inspection of the stands and their location suggests that it is reasonably correct.

Comparing the three logging-road communities by a coefficient of community based on frequencies (F) and cover (C) indicates the following:

		Site 1 50–150 m (R2)	Control area (CR)
Site 1			
0–50 m (R1)	F	82.4	70.1
	C	65.0	58.3
50–150 m (R2)	F		62.9
	C		40.4

These indices indicate that the three communities were very similar in terms of frequencies but less so in terms of cover. The CC of 40.5 for the last pair was quite low.

Table 20

COEFFICIENT OF COMMUNITY (CC) AMONG NINE STANDS BASED ON FREQUENCY (F), DENSITY (D), AND BASAL AREA (B) OR COVER (C) OF TREES, SHRUBS, AND GROUND VEGETATION

		Aspen			Birch			Northern hardwood		
		Site 1			Site 1			Site 1		
		0–50 m (A1)	50–150 m (A2)	Control (CA)	0–50 m (B1)	50–150 m (B2)	Control (CB)	0–50 m (NH1)	50–150 m (NH2)	Control (CNH)
						Trees				
A1	F		58.0	76.0	80.8	60.1	38.3	64.7	39.3	39.5
	D		54.7	75.6	65.2	40.5	19.7	47.4	14.4	15.6
	B		75.4	84.3	75.4	44.2	21.3	51.3	28.8	19.2
A2	F			72.0	62.5	55.5	42.2	58.1	33.7	36.8
	D			68.1	63.7	55.5	33.8	47.7	22.1	28.3
	B			76.0	64.2	43.7	25.2	45.6	25.9	20.0
CA	F				73.1	67.6	54.9	62.4	41.6	50.0
	D				67.9	55.3	26.4	53.5	19.7	21.4
	B				66.2	39.3	23.0	44.2	26.3	18.1
B1	F					72.0	47.2	78.0	53.1	50.2
	D					60.4	31.3	75.2	32.6	29.7
	B					57.7	27.0	71.9	37.0	24.8
B2	F						67.6	71.2	58.4	64.9
	D						53.7	61.1	27.1	47.7
	B						59.9	64.0	54.4	61.4
CB	F							51.6	64.2	79.7
	D							34.8	42.5	61.7
	B							28.2	45.6	63.1
NH1	F								59.0	54.4
	D								41.3	33.1
	B								47.2	28.9
NH2	F									66.2
	D									68.2
	B									49.9
						Shrubs				
A1	F		48.0	60.8	81.1	54.0	21.4	63.8	26.5	4.2
	D		27.9	58.0	66.4	49.4	5.9	40.7	14.1	6.6
	B		30.6		68.0	58.7		72.8	24.8	
A2	F			45.7	47.7	44.9	21.0	36.5	23.5	7.9
	D			30.6	37.7	41.5	8.6	33.3	17.9	2.5
	B				42.8	45.8		29.6	36.4	
CA	F				60.7	41.6	36.4	67.3	41.0	11.8
	D				71.8	54.3	16.1	66.4	32.4	4.8
	B									
B1	F					56.3	20.6	63.6	31.2	8.1
	D					63.7	8.8	55.1	21.8	2.3
	B					82.2		76.5	41.7	
B2	F						32.4	46.8	39.8	9.8
	D						14.1	61.3	31.6	2.3
	B							61.9	53.5	
CB	F							31.7	60.0	40.0
	D							16.8	47.1	33.3
	B									
NH1	F								40.0	6.2
	D								36.4	1.8
	B								34.8	

Table 20 (Continued)

		Aspen			Birch			Northern hardwood		
		Site 1			Site 1			Site 1		
		0–50 m (A1)	50–150 m (A2)	Control (CA)	0–50 m (B1)	50–150 m (B2)	Control (CB)	0–50 m (NH1)	50–150 m (NH2)	Control (CNH)
NH2	F									33.3
	D									27.1
	B									
					Ground Vegetation					
A1	F		59.8	58.4	73.8	62.9	37.5	67.0	45.7	35.9
	C		59.5	54.9	63.8	49.0	53.0	66.9	37.8	28.6
A2	F			52.5	57.9	64.3	38.4	63.2	47.8	38.0
	C			41.9	39.3	34.6	36.2	37.8	26.4	16.4
CA	F				59.5	57.3	50.3	60.1	51.7	45.8
	C				35.2	27.0	53.0	42.7	25.6	36.4
B1	F					65.7	38.6	68.2	48.7	40.1
	C					73.2	47.7	70.5	52.5	43.1
B2	F						47.8	61.8	63.7	53.8
	C						39.6	59.5	65.5	52.0
CB	F							42.4	51.3	66.0
	C							47.6	38.7	61.5
NH1	F								59.2	45.2
	C								55.8	40.8
NH2	F									69.0
	C									59.7

Table 21

INDEX OF DIVERSITY* (ID) AND EQUITABILITY† (E) OF 12 PLANT COMMUNITIES

Type of community	Trees ID	Trees E	Shrubs ID	Shrubs E	Ground vegetation ID	Ground vegetation E	All strata ID	All strata E
Site 1 (0–50 m)								
Aspen (A1)	2.35	0.60	1.04	0.27	3.34	0.52	4.22	0.62
Birch (B1)	2.74	0.68	1.52	0.36	3.73	0.60	4.37	0.69
Northern hardwood (NH1)	3.18	0.75	1.06	0.29	3.30	0.53	4.54	0.68
Logging road (R1)							4.49	0.74
Site 1 (50–150 m)								
Aspen (A2)	2.33	0.56	3.40	0.76	3.23	0.52	4.29	0.63
Birch (B2)	2.52	0.70	1.27	0.35	3.27	0.55	3.61	0.56
Northern hardwood (NH2)	2.77	0.75	1.37	0.41	2.38	0.44	3.64	0.60
Logging road (R2)							4.58	0.82
Control area								
Aspen (CA)	2.02	0.56	1.53	0.48	2.16	0.39	3.27	0.54
Birch (CB)	1.73	0.58	1.12	0.71	1.70	0.40	2.75	0.56
Northern hardwood (CNH)	1.87	0.62	1.91	0.96	1.40	0.30	2.57	0.49
Logging road (CR)							4.82	0.86

*The Shannon and Weaver index of diversity (Shannon, 1948): $ID = -\Sigma\, p_i \log_2 p_i$.

†Equitability or evenness (Pielou, 1969): $E = ID/\log_2 s$, where ID is index of diversity and s is number of species in a community.

The Shannon–Weaver index of diversity (ID) (Shannon, 1948) and the equitability or evenness (E) (Pielou, 1969) based on the cover of individual species were calculated for all 12 communities to compare their floristic richness (Table 21). Both ID and E values for pooled vegetational strata of the nine forest stands correlate well with the two-dimensional ordination (Fig. 1). The average ID and E values of the five stands clustered in the "cool and wet" corner were high (4.17 and 0.63). These values were intermediate for the two stands in the center (3.62 and 0.58) and low for the two stands in the "dry and warm" corner of the diagram (2.66 and 0.52). The ID and E values of the three logging-road communities were among the highest and were very similar among themselves.

CLASSIFICATION OF PLANT COMMUNITIES

As stated previously, the main objective of this study was to describe, com-

Table 22

CLASSIFICATION OF NINE STANDS IN SITE 1 AND THE CONTROL AREA

Location and forest type in use	Nearest equivalent in classification systems		
	SAF (1954)	Ohmann and Ream (1971)	Curtis (1959)
Site 1 (0–50 m)			
Aspen (A1)	Aspen (No. 16)	Aspen–birch or maple–aspen–birch	Boreal or lowland wet–mesic
Birch (B1)	Transitional; aspen–paper birch (No. 11)	Maple–aspen–birch	Boreal or lowland wet–mesic
Northern hardwood (NH1)	Transitional; aspen–paper birch (No. 11)	Maple–aspen–birch	Boreal or lowland wet–mesic
Site 1 (50–150 m)			
Aspen (A2)	Aspen (No. 16) or aspen–paper birch (No. 11)	Aspen–birch	Boreal or lowland wet–mesic
Birch (B2)	Transitional; aspen–paper birch (No. 11)	Maple–aspen–birch	Upland dry–mesic
Northern hardwood (NH2)	Sugar maple–american basswood (No. 26)	No equivalent	Upland mesic
Control area			
Aspen (CA)	Aspen (No. 16) or aspen–paper birch (No. 11)	Aspen–birch	Boreal or lowland wet–mesic
Birch (CB)	Paper birch (No. 18)	No equivalent	Upland dry–mesic
Northern hardwood (CNH)	Transitional; similar to paper birch (No. 18), white pine–northern red oak–white ash (No. 20), and sugar maple–basswood (No. 26)	No equivalent	Upland dry–mesic

pare, and classify the plant communities selected for the gamma-irradiation experiment to provide a basis for quantifying their structural and compositional changes following the radiation treatment. The evidence presented here indicates that, depending on the classification system used for comparison, four to six different cover types were present in site 1 and the control area (Table 22) and that the initial classification of these areas as aspen, birch, and northern hardwood types was only partially correct.

The aspen type, which corresponds to the SAF forest cover type No. 16 (Society of American Foresters, 1954), was found only in the aspen segment of the 50-m circle in site 1. The other two communities tentatively called aspen were intermediate between the aspen and aspen–paper birch cover types (SAF Nos. 16 and 11). If the heavy representation of red maple is considered, they could be called maple–aspen–birch forest types, as suggested by Ohmann and Ream (1971). These communities grow on moist sites and fit into the boreal or lowland wet–mesic group of northern forests described by Curtis and his coworkers (1959).

Among the communities initially called birch, only the control birch stand was a typical paper birch (SAF No. 18). The two birch communities of site 1 were transitional, approaching the aspen–paper birch cover type (SAF No. 11). The stand within the 50-m circle is located on a wet plateau containing a depression that remains flooded for most of the growing season. This stand was tentatively placed among the boreal or lowland wet–mesic northern forests. The other two birch communities fit among the upland dry–mesic forests of Curtis's (1959) continuum.

The three northern hardwood communities were the most variable and the most difficult to classify. They had a high proportion of sugar maple and paper birch, with basswood, red maple, red oak, ironwood, and quaking aspen as important associates. The community within the 50-m circle in site 1 grows on a wet site that remains flooded for a part of the growing season. It resembled the aspen–paper birch (SAF No. 11) or maple–aspen–birch (Ohmann and Ream, 1971) type and fit among the lowland or boreal wet–mesic forests of Curtis (1959). The northern hardwood community outside that area, which can be classified as a sugar maple–basswood cover type (SAF No. 26), fell among the mesic forests in Curtis's continuum. The control northern hardwood stand was apparently transitional and resembled at least three cover types in the SAF classification system (Table 22). This was the second most mesic community of the area but had not reached a stand index value set by Curtis (1959) for the mesic northern forests.

The sampled communities contained many different species but only a few were outstanding. Importance values for the total vegetation in site 1 provided a way of comparing and ranking the individual species (Table 23). Importance values (IV) of the most important species were obtained by the formula of Curtis and McIntosh (1951):

$$IV = \frac{RF + RD + RBA(\text{or } RC)}{3}$$

Table 23

IMPORTANCE VALUES (IV) OF TOTAL VEGETATION IN SITE 1

Species	Scaled IV			Total IV	Total IV adjusted to 100
	Trees	Shrubs	Ground vegetation		
Populus tremuloides	21.1	0.4	0.1	21.6	12.5
Acer rubrum	18.3	0.6	0.7	19.6	11.3
Betula papyrifera	15.9	0.2	0.1	16.2	9.4
Acer saccharum	12.7	0.4	0.5	13.6	7.9
Corylus cornuta		7.3	1.9	9.2	5.3
Carex pensylvanica			7.4	7.4	4.3
Aster macrophyllus			6.8	6.8	3.9
Quercus rubra	5.5	0.2	<0.1	5.8	3.4
Pteridium aquilinum			5.5	5.5	3.2
Fraxinus sp.	4.0	0.3	<0.1	4.4	2.5
Prunus serotina	3.3	0.3	0.5	4.1	2.4
Tilia americana	3.7	0.1	<0.1	3.8	2.2
Ostrya virginiana	3.3	0.1	<0.1	3.4	2.0
Amelanchier sp.	1.6	1.0	0.5	3.1	1.8
Oryzopsis asperifolia			3.0	3.0	1.7
Aralia nudicaulis			2.7	2.7	1.6
Abies balsamea	2.4	0.2	<0.1	2.6	1.5
Rubus allegheniensis		0.9	1.1	2.0	1.2
Athyrium filix-femina			1.7	1.7	1.0
Viola incognita			1.6	1.6	0.9
Anemone quinquefolia			1.4	1.4	0.8
Lycopodium obscurum			1.3	1.3	0.8
Cornus canadensis			1.2	1.2	0.7
Subtotal	91.8	12.0	38.1	142.0	82.3
Total	100.0	14.4	58.3	172.7	100.0

where RF, RD, and RBA(or RC) refer to relative values of frequency, density, and basal area or cover of a species. To assess the total IV of a tree or shrub species present in two or three strata, we calculated IV's for each stratum separately, scaled them by the average cover value of that stratum, and summed them. The average cover values were 1.00 (or 100%), 0.144 (or 14.4%), and 0.583 (or 58.3%) for the tree, shrub, and ground-vegetation stratum, respectively. Finally, the total IV's were adjusted to 100 (Table 23). Four tree species headed the list, quaking aspen, paper birch, and red and sugar maple; these were followed by beaked hazel and two herbs, *C. pensylvanica* and large-leaved aster. Among the top 23 species on the list were 11 trees, 2 shrubs, and 10 herbs. Only one conifer, balsam fir, was among them; two other conifers at site 1 were insignificant. These top 23 accounted for more than 82% of the adjusted importance values.

Two of the important tree species, quaking aspen and paper birch, are typical of early successional stages in forests devastated by some natural agent, such as fire, or by logging (Curtis 1959). The high resprouting potential of aspen, an abundant production of lightweight birch seeds that are disseminated by the wind, and a rapid juvenile growth of both give these two species a dominating advantage over other native tree species. Their dominance is for one generation only, however; they usually do not succeed themselves and with time are replaced by various more permanent members of the northern forest, such as sugar and red maple, balsam fir, basswood, white ash, and red oak.

Seven of the nine stands were dominated or codominated by aspen and/or paper birch, and the remaining two stands had high proportions of at least one of these species. Within the 50-m area, aspen and paper birch jointly comprised 51% and red maple 22% of the dominant–codominant trees. Thickets of young aspen and well-distributed young red and sugar maples suggest the forest composition in the next 20 to 50 years. Seedlings of sugar and red maple, balsam fir, black cherry, and black ash were present in sufficient numbers in the ground layer to form a future forest composed of these species. The aspen stand in the 50- to 150-m area is likely to develop into a forest composed of red maple, balsam fir, black cherry, and red oak since these species were present in the shrub and ground-vegetation layers of this community. The future composition of the aspen stand in the control area will be less diverse, with red maple as the main component and black cherry and aspen as important associates. The present and future composition of the birch stand in the 50- to 150-m area resembles the birch and northern hardwood stands within the 50-m area. This community eventually should be dominated by such species as red and sugar maple, white ash, balsam fir, red oak, and black cherry because seedlings of all these were present. The future composition of the only true birch cover type of the control area will be different. White ash will probably dominate the area, with sugar maple and black cherry as its main associates.

The two remaining communities were originally classified as northern hardwood forest types. Their present 52% CC is likely to increase with time since in both stands the most abundant among young saplings, shrublike stems, and tree seedlings were sugar maple, white ash, black cherry, red oak, and paper birch.

These projections are based on the assumption that the stands will develop without any major disruption by natural or man-made factors. The successional process may be interrupted or even permanently stopped if the communities are destroyed during their early successional stages. Such a process is exemplified by a silviculture method aimed at producing primarily aspen by logging the stands before they reach the more-advanced successional stages. Gamma irradiation is likely to produce similar effects within the effective radiation range.

No attempt was made to classify the logging-road vegetation. Its floristic composition was similar to old-field vegetation or to vegetation that develops in disturbed areas and waste places. The wide ecological range of many of the component species indicates that they tolerate and are able to develop in a variety of environments. In view of the reported high radioresistance of these

species (Woodwell and Oosting, 1965), they provide desirable experimental material for the planned radiation study.

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Physical Condition and Dimensions of Trees in Site 1 and the Control Area

7

J. ZAVITKOVSKI
Institute of Forest Genetics, North Central Forest Experiment Station, Forest Service, U. S. Department of Agriculture, Rhinelander, Wisconsin

ABSTRACT

Physical conditions of trees composing nine forest communities of the Enterprise Radiation Forest are described and relationships between their age, size, and crown dimensions are established. The trees, mostly of vegetative origin, were reasonably healthy and free of serious mechanical damage. They varied widely in age, size, and crown dimensions, but for individual species good relationships existed among these variables. It is concluded that the trees and the nine forest stands provide suitable and biologically interesting study material for a pilot study on the effects of ionizing radiation on natural forest ecosystems.

This paper summarizes information on the physical condition of trees in the nine forest communities of site 1 and the control area, which are described in Chap. 6, and establishes relationships among some variables, including tree age, size, and crown dimension. These data may provide supporting evidence for predicting and explaining the radiation response in these forest communities. Detailed information was gathered on trees within the expected effective radiation range of 50 m from the site center. With minor adjustments, this information also applies to trees outside that range in site 1 and the control area.

Relationships between some physical parameters and the degree of radiation damage to trees of the same species have been reported in various radioecological studies (Woodwell and Rebuck, 1967; Miller, 1968; McCormick, 1969). Describing radiation damage to an oak–pine forest on Long Island, Woodwell and Rebuck noted that both pine and oak trees with large crowns were more radioresistant than individuals with small crowns. Similar trends were found by McCormick in an irradiated longleaf and slash pine forest in Georgia, but contradictory evidence from the same area was reported by Miller, who observed a negative relation between the size of young longleaf pine trees and their radioresistance. In the tropical rain forest of Puerto Rico, Smith (1970) reported that canopy trees died at approximately the same distance from the radiation source as understory individuals. This indicates that the larger canopy trees were more radiosensitive than the smaller understory individuals because their canopies, which are considered the main interceptors of radiation damage, occupied the space higher above the ground where, for the same distance from the source, the radiation dose was the lowest (McCormick, 1970).

METHODS

The nine forest stands and their locations in the Enterprise Radiation Forest are described in Chaps. 2 and 6. All trees with a diameter at breast height (dbh) larger than 2.5 cm were included in the survey. Their dbh, height, crown length, and crown width were measured from the ground using metric tapes and Haga hypsometers. The tree characteristics described were:

1. Tree position: dominant, codominant, intermediate, or suppressed.
2. Type of stem: single, forked, or clustered.
3. Disease and insect damage.
4. Mechanical damage.

Age was based on increment cores extracted about 25 cm above the ground from 202 trees randomly selected within 50 m from the site center.

Relations between tree age as an independent variable and dbh and height as dependent variables were described by a growth function, $Y = a(1 - e^{bx})^c$, which was also fitted to dbh and height data forcing the curve through a height of 1.37 cm (breast height) at dbh = 0. Relations between dbh and crown width, dbh and crown volume, and tree height and crown length were approximated by a function

$$Y = a + b \exp\left[-\left|\frac{(X/X_p) - 1}{(X_i/X_p) - 1}\right|^n\right] \quad (1)$$

(Jensen and Homeyer, 1970). Both models were fitted to the data by a combination of graphic and least-squares methods.

RESULTS

Physical Condition

The average age of the 202 sample trees was 24.4 years, with a relatively high standard deviation of 10.4 years (Table 1). The age varied widely among as well as within the species. The oldest trees sampled were 70 to 80 years old, and the youngest were about 5 years old. Average age ranged from 45.8 years for red oak (*Quercus rubra*) to 11.7 years for willow (*Salix* sp.). The age of quaking aspen (*Populus tremuloides*), the most important species in the radiation forest, ranged from 6 to 41 years, with an average of 16.7 years. Three other important tree species, red and sugar maple (*Acer rubrum* and *A. saccharum*) and

paper birch (*Betula papyrifera*) had above-average ages.

Ages of trees beyond the 50-m perimeter and in the control area were not determined, but subjective observations indicated that they were within the limits determined for trees within 50 m from the site center.

The high variability in tree ages was reflected in the dbh distribution of trees by species within 50 m from the site center (Table 2). Very high variability in dbh was present in quaking aspen, black cherry (*Prunus serotina*), sugar maple, and paper birch. Net dbh change for all important species was based on data for average dbh in 1969 and 1970. On the average, the dbh increased by 0.35 cm in one year; this is a 4.2% increase. Above-average dbh increases were determined for quaking aspen and paper birch.

In all nine stands the proportion of dominant trees was smallest and that of suppressed trees was largest (Table 3). The dominant and codominant trees composing the main canopy accounted for 18.3 to 36.4% of the total number of trees.

Distinct species characteristics were evident in the distribution of trees among three stem-type classes (Tables 3 and 4). In the aspen communities (A1, A2, and CA), the high proportion of single stems can be traced to quaking aspen, which almost always occurs as a single-stemmed tree. Physical characteristics of aspen trees indicated that they were of vegetative origin and occurred in clones of various sizes. Although delineation of the clones would be desirable, it was beyond the scope of this survey. A high proportion of tree clusters in the northern hardwood and birch forest types points to the vegetative origin of these stands as well. In red maple, juneberry (*Amelanchier* sp.), yellow birch (*Betula alleghaniensis*), ironwood (*Ostrya virginiana*), willow, and American basswood (*Tilia americana*), almost two-thirds of all trees occurred in clusters or as forks (Table 4).

In general, trees in the nine stands were healthy; 79.4 to 94.0% had no visible evidence of disease or insect damage (Table 3). Fungous infection was the most common disease among the affected trees. About one-third of all trees in site 1 and 12% in the control area had some mechanical damage (Table 3). Scars and broken tops or limbs were the most common types of damage.

Table 1

AVERAGE AGE OF SELECTED TREE SPECIES WITHIN 50 m FROM THE SITE CENTER

Species	Number of trees sampled	Average age, years	SD*	Range of age, years
Abies balsamea	2	36.0	5.7	32 to 40
Acer rubrum	49	27.6	9.0	11 to 46
A. saccharum	20	31.6	13.6	16 to 43
Amelanchier sp.	4	22.8	11.3	5 to 40
Betula alleghaniensis	3	17.3	8.4	12 to 27
B. papyrifera	16	33.2	13.7	5 to 49
Fraxinus nigra	14	31.4	13.2	6 to 49
Ostrya virginiana	3	21.7	7.6	13 to 27
Populus tremuloides	61	16.7	8.4	6 to 41
Prunus serotina	7	30.7	10.6	19 to 45
Quercus rubra	5	45.8	14.4	32 to 70+
Salix sp.	7	11.7	5.1	5 to 19
Tilia americana	5	28.8	4.6	23 to 33
Other species	6	21.5	11.4	10 to 39
Total	202	24.4	10.4	5 to 70+

*Standard deviation.

Table 2

DIAMETER AT BREAST HEIGHT (DBH) OF SELECTED SPECIES WITHIN 50 m FROM THE SITE CENTER

Species	1969			1970			Net dbh change, cm	Percent dbh change
	Mean, cm	SD*	Number of trees	Mean, cm	SD*	Number of trees		
Abies balsamea	13.86	7.79	14	14.21	7.85	14	0.35	2.5
Acer rubrum	8.39	4.72	410	8.74	4.74	410	0.35	4.2
A. saccharum	8.13	5.34	133	8.39	5.41	133	0.26	3.2
Amelanchier sp.	4.85	2.43	30	5.05	2.21	30	0.20	4.1
Betula alleghaniensis	5.02	3.15	26	5.32	3.24	26	0.30	6.0
B. papyrifera	12.37	6.82	146	12.78	6.69	146	0.41	3.3
Fraxinus nigra	8.21	4.65	126	8.57	4.43	126	0.36	4.4
Ostrya virginiana	7.41	2.72	50	7.62	2.67	50	0.21	2.8
Populus tremuloides	6.88	5.67	535	7.28	5.76	535	0.40	5.8
Prunus serotina	10.24	7.82	54	10.55	7.74	54	0.31	3.0
Quercus rubra	21.27	10.55	17	21.22	10.72	17	−0.05†	−0.02†
Salix sp.	3.40	1.30	38	3.61	1.31	38	0.21	6.2
Tilia americana	9.94	5.02	47	10.26	4.98	47	0.32	3.2
Mean for all trees	8.22	5.85	1663	8.57	5.89	1672	0.35	4.2

*Standard deviation.
†Reflects mortality and ingrowth.

Relationships Between Tree Dimensions

Relations between age as an independent variable and dbh and height were established for quaking aspen, paper birch, and red and sugar maple trees growing within approximately 50 m from the site center (Figs. 1 to 3). The age–dbh regressions indicated that the aspen stems with a dbh of 5 cm were about 11 years old, but the corresponding dbh in paper birch and maples was reached at 15 and 20 years, respectively. Quaking aspen grew rapidly for at least 40 years, when the average tree attained a dbh of about 21 cm. Paper birch needed 6 more years and maples 18 more years to reach that size.

Quaking aspen grew the most rapidly in height, reaching 5, 10, and 15 m at 7, 16, and 29 years, respectively. The corresponding ages for these heights in paper birch were about 10, 22, and 36 years and in maples 11, 24, and 46 years. The dominant individuals of all four species reached these heights 5 to 15 years earlier than the intermediate and suppressed trees.

Table 3

PERCENTAGE OF TREES IN NINE STANDS HAVING CHARACTERISTICS DESCRIBED (WINTER 1969/1970)

Tree characteristic	Site 1, 0–50 m, A1*	B1*	NH1*	50–150 m, A2*	B2*	NH2*	Control area, CA*	CB*	CNH*
Position									
Dominant	4.6	2.3	2.8	1.8	2.0	0.8	16.3	8.4	4.3
Codominant	13.7	26.6	24.6	20.3	22.9	24.3	20.1	18.6	21.2
Intermediate	20.0	16.4	18.5	17.4	11.5	11.9	31.2	30.6	24.1
Suppressed	61.7	54.7	54.1	60.5	63.6	63.0	32.4	42.4	50.4
Type of stem									
Single	78.8	65.3	58.0	67.3	45.6	57.8	70.6	54.6	54.9
Forked	3.7	5.5	11.2	2.6	7.8	4.4	13.3	27.2	20.9
Clustered	17.5	29.2	30.8	30.1	46.6	37.8	16.1	18.2	27.2
Disease or insect damage									
None	87.6	85.7	89.1	87.2	79.4	91.1	82.0	93.5	94.9
Disease	12.2	14.3	10.9	11.2	17.1	8.9	18.0	6.5	5.1
Insect damage	0.2			1.4	2.6				
Combination				0.2	0.9				
Mechanical damage									
None	67.4	72.8	67.8	69.4	66.2	69.9	85.6	85.2	89.3
Broken top or limb	3.2	2.4	2.7	3.2	2.2	2.7	14.4	11.1	3.7
Scar	18.1	21.2	22.0	23.4	26.6	23.5		2.8	4.8
Bent or uprooted	6.5	1.8	3.4	1.8	3.4	1.9		0.6	0.3
Combination	4.8	1.8	4.1	2.3	1.6	2.0		0.3	1.9

*Abbreviations identify transects in the three areas: A1, aspen; B1, birch; and NH1, northern hardwood transects within 50 m from the site center. A2, aspen; B2, birch; and NH2, northern hardwood transects 50 to 150 m from the site center. CA, aspen; CB, birch; and CNH, northern hardwood transects in the control area.

Table 4

NUMBERS OF SINGLE, FORKED, AND CLUSTERED TREES OF SELECTED SPECIES WITHIN APPROXIMATELY 50 m FROM THE SITE CENTER

Species	Tree classes: Single	Forks	Clusters	Total
Abies balsamea	13	4	0	17
Acer rubrum	195	77	251	523
A. saccharum	89	10	56	155
Amelanchier sp.	8	2	20	30
Betula alleghaniensis	8	7	15	30
B. papyrifera	112	17	44	173
Fraxinus nigra	104	10	27	141
Ostrya virginiana	19	1	38	58
*Populus tremuloides**	569	0	0	569
Prunus serotina	37	4	15	56
Quercus rubra	12	9	2	23
Salix sp.	17	11	16	44
Tilia americana	18	0	31	49
9 other species	116	1	14	131
Total	1317	153	529	1999
Percent of total	65.9	7.6	26.5	

*No attempt was made to identify trees of each individual clone.

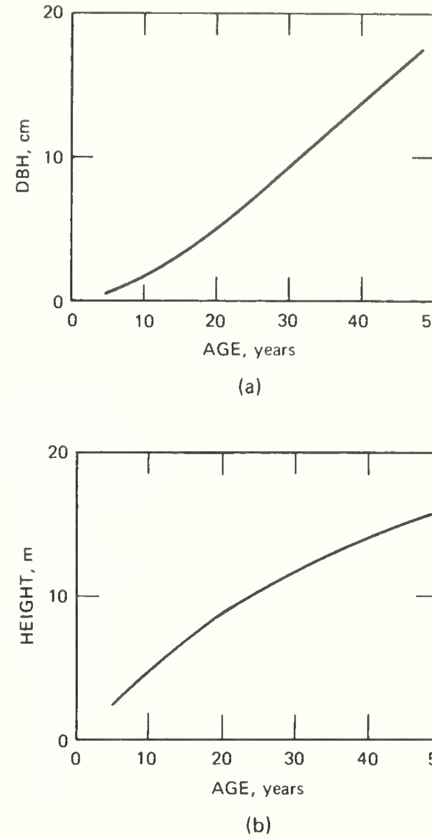


Fig. 1 Relation between age and dbh and height of *Acer rubrum* and *A. saccharum*. R^2 is index of determination.
(a) $Y = 50(1 - e^{-0.0175X})^{1.875}$
$R^2 = 0.738$
SE = 2.79
N = 66
(b) $Y = 25(1 - e^{-0.0195X})^{0.945}$
$R^2 = 0.553$
SE = 2.43
N = 66

Regressions of height over dbh of most species growing within 50 m from the site center, including red and sugar maples, paper birch, quaking aspen, red oak, and American basswood, were very similar (see Figs. 4 to 13). For the same dbh their average heights varied less than ±10%. Different relationships between these parameters were apparent in balsam fir (*Abies balsamea*), black ash (*Fraxinus nigra*), and black cherry.

From the standpoint of radioecology, crown dimensions are probably more important than the other tree dimensions. Relations between dbh and crown width, tree height and crown length, and dbh and crown volume varied widely in most species (Table 5). For the same dbh crowns of red oak and red and sugar maples were the widest, and those of balsam fir, black ash, and black cherry were the narrowest (see Figs. 14 to 22 and Table 6). In relation to tree height, balsam fir had by far the longest crowns, and black cherry had the shortest (Table 6). Crown dimensions were used to calculate crown volumes because

volumes may be a better criterion for evaluating potential radiosensitivity than the linear dimensions are. Crown volumes were calculated using a formula for the volume of a paraboloid:

$$A = \frac{\pi}{8} CW^2 \times CL \qquad (2)$$

where V is the volume (m^3), CW is the crown width (m) and CL is the crown length (m). Finally, crown volumes were related to tree dbh (Figs. 14 to 22).

In relation to dbh crown volumes of red oak were consistently the largest (Table 6). Red and sugar maples also had large crowns, but crowns of black cherry, paper birch, quaking aspen, black ash, and American basswood were small. These comparisons must be interpreted cautiously because of the variability of the data, the inadequacies of the growth models used to relate the dimensions, and, in some species, a small or unequally distributed (lopsided) sample size.

DISCUSSION

Results of the survey show that the trees composing the nine forest communities have two striking characteristics: They are mostly healthy and free of mechanical damage, and they vary greatly in all estimated physical parameters. The first characteristic is very desirable for biological experimentation, but the second is usually undesirable and is especially bothersome when quantitative responses to an artificial stress are measured. In this initial study, however, the variability in age, size, and crown dimensions may be an asset because variability will make it possible to evaluate a greater range of relations between plant characteristics and their radiosensitivity. The age of most species ranges from young to mature individuals, and tree sizes and crown dimensions spread over a wide range of values. Both these factors provide good bases for critical evaluation of some controversial interactions between these variables and radiosensitivity (Woodwell and Rebuck, 1967; Miller, 1968; McCormick, 1969; Smith, 1970). Stand homogeneity will be important in future experiments on the effects of radiation stress on ecosystem productivity, but for the pilot study the selected stands provide suitable and biologically interesting study material.

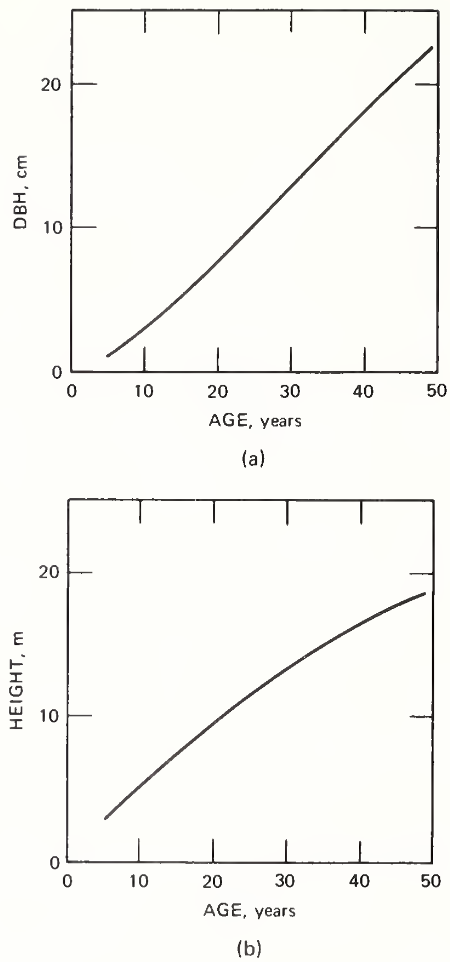


Fig. 2 Relation between age and dbh and height of *Betula papyrifera*.
(a) $Y = 50(1 - e^{-0.0195X})^{1.665}$
$R^2 = 0.794$
SE = 3.60
N = 16
(b) $Y = 27(1 - e^{-0.0245X})^{1.105}$
$R^2 = 0.721$
SE = 3.12
N = 16

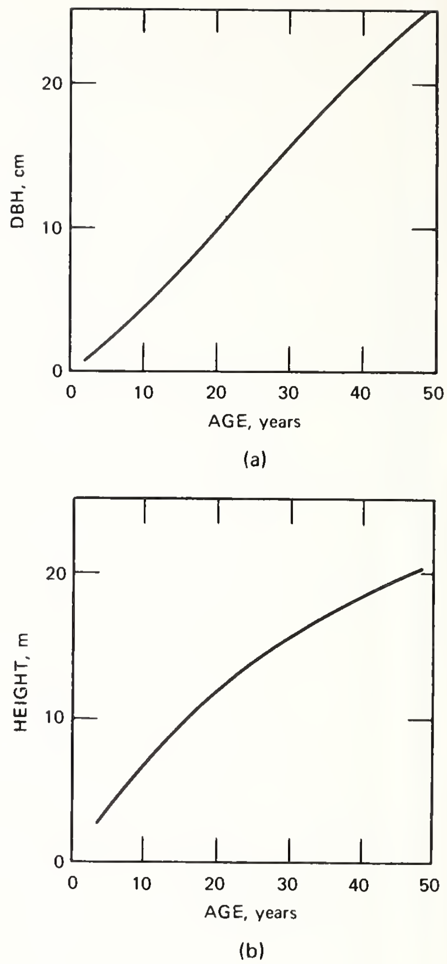


Fig. 3 Relation between age and dbh and height of *Populus tremuloides*.
(a) $Y = 50(1 - e^{-0.0205X})^{1.495}$
$R^2 = 0.813$
SE = 2.21
N = 61
(b) $Y = 27(1 - e^{-0.0295X})^{1.001}$
$R^2 = 0.711$
SE = 2.23
N = 61

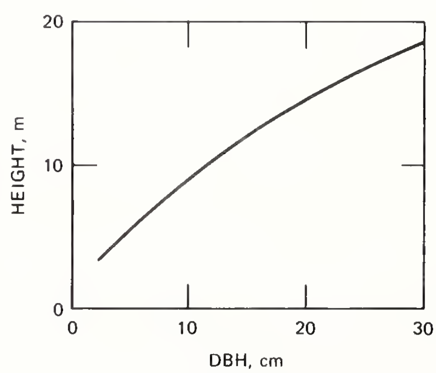


Fig. 4 Relation between dbh and height of *Abies balsamea*.
$Y = 1.37 + 24(1 - e^{-0.045X})^{1.12}$
$R^2 = 0.949$
SE = 1.10
N = 17

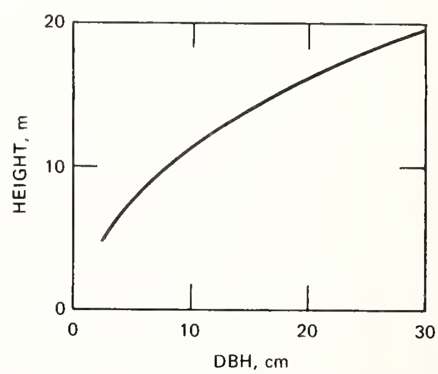


Fig. 5 Relation between dbh and height of *Acer rubrum*.
$Y = 1.37 + 24(1 - e^{-0.032X})^{0.744}$
$R^2 = 0.855$
N = 470

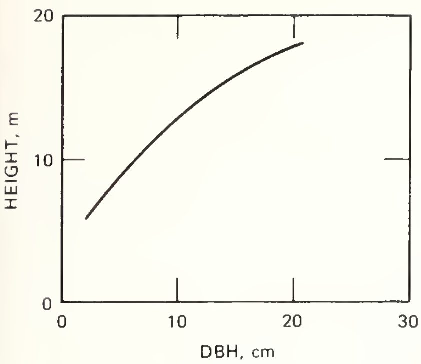


Fig. 6 Relation between dbh and height of *Acer saccharum.*

$Y = 1.37 + 26(1 - e^{-0.030X})^{0.650}$
$R^2 = 0.787$
N = 143

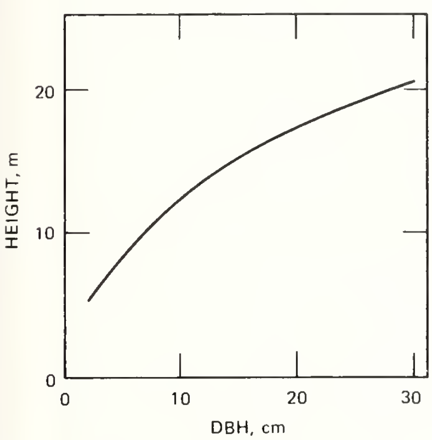


Fig. 7 Relation between dbh and height of *Betula papyrifera.*

$Y = 1.37 + 26(1 - e^{-0.035X})^{0.770}$
$R^2 = 0.888$
N = 159

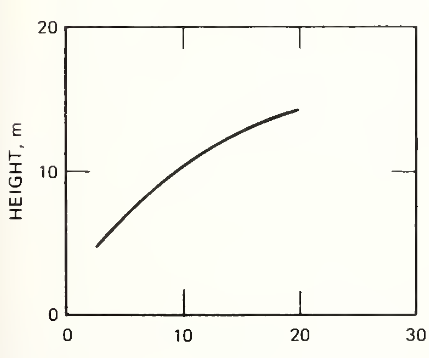


Fig. 8 Relation between dbh and height of *Fraxinus nigra.*

$Y = 1.37 + 19(1 - e^{-0.051X})^{0.905}$
$R^2 = 0.860$
N = 119

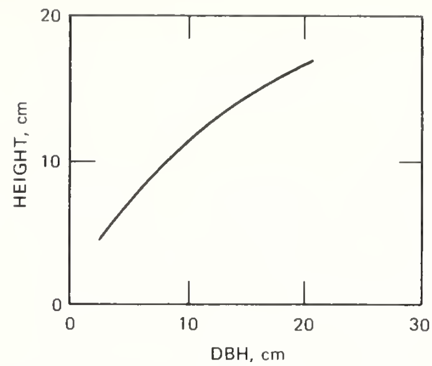
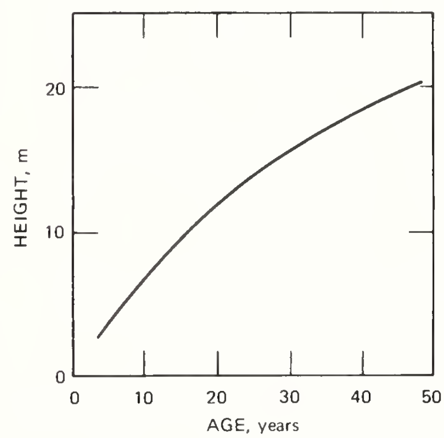


Fig. 9 Relation between dbh and height of *Ostrya virginiana.*

$Y = 1.37 + 20(1 - e^{-0.071X})^{0.995}$
$R^2 = 0.723$
N = 47



(b)

Fig. 10 Relation between dbh and height of *Populus tremuloides.*

$Y = 1.37 + 26(1 - e^{-0.035X})^{0.753}$
$R^2 = 0.916$
N = 508

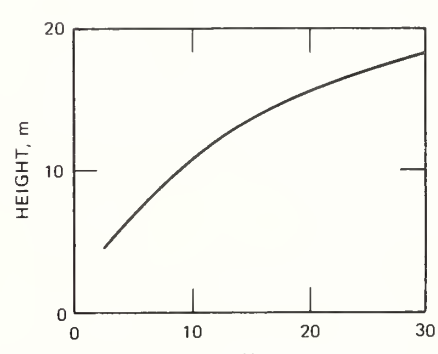


Fig. 11 Relation between dbh and height of *Prunus serotina.*

$Y = 1.37 + 21(1 - e^{-0.054X})^{0.985}$
$R^2 = 0.923$
N = 44

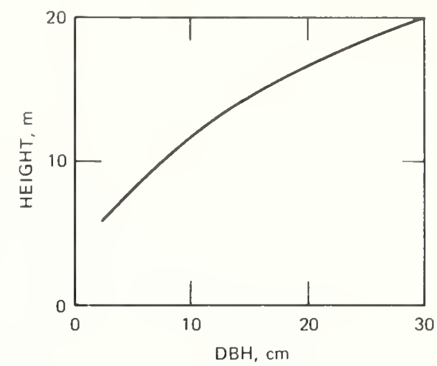


Fig. 12 Relation between dbh and height of *Quercus rubra.*

$Y = 1.37 + 25(1 - e^{-0.035X})^{0.750}$
$R^2 = 0.911$
N = 22

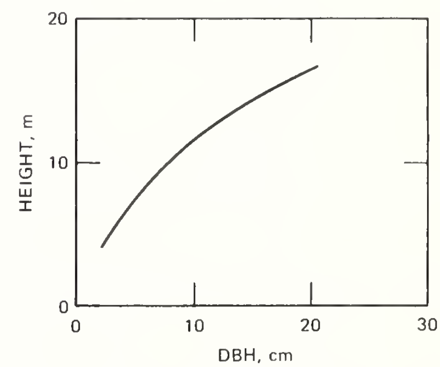


Fig. 13 Relation between dbh and height of *Tilia americana.*

$Y = 1.37 + 26(1 - e^{-0.035X})^{0.827}$
$R^2 = 0.895$
N = 39

An added asset of these stands is their mostly vegetative origin; this can be inferred from the high incidence of trees occurring in clusters in the northern hardwood forest type and the root-sprouting habit of aspens. Since both cluster trees and aspen clones are genetically identical, their uniform response or lack of response to radiation should provide a more reliable basis for drawing conclusions in these experiments.

The predicted LD_{50} of the deciduous trees of the radiation forest ranged from 110 to 480 r/day for one growing season (Chap. 13, this volume), but a much narrower LD_{50} range (from 170 to 305 r/day for one season*) was determined for the four most important tree species (quaking aspen, paper birch, and

*The LD_{50} range may be even narrower (205 to 305 r) if the higher somatic chromosome number (2n = 104) prevails in red maple.

Table 5

CROWN DIMENSIONS, PROJECTED AREA, AND VOLUME FOR SELECTED TREE SPECIES WITHIN 50 m FROM THE SITE CENTER

Species	No. of trees	Crown								Cumulative crown	
		Length, m		Width, m		Projected area,* m^2		Volume,† m^3		Projected area,* m^2	Volume,† m^3
		Mean	SD‡	Mean	SD	Mean	SD	Mean	SD		
Trees with dbh of 2.5 to 10.0 cm											
Abies balsamea	5	4.9	1.1	2.7	0.7	6.1	2.9	16.1	10.1	30	81
Acer rubrum	280	4.1	1.9	2.9	1.0	7.4	5.4	17.9	19.1	2072	5,012
A. saccharum	97	4.6	2.2	3.5	1.2	10.7	8.2	30.3	36.0	1038	2,939
Amelanchier sp.	30	2.9	1.2	2.6	0.8	5.7	3.2	9.3	8.8	172	279
Betula alleghaniensis	23	3.0	1.2	2.8	1.0	6.9	5.1	11.4	11.5	159	262
B. papyrifera	61	3.5	1.5	2.5	0.7	5.3	3.1	10.1	8.5	322	614
Fraxinus americana	4	2.3	1.4	2.5	0.5	5.0	1.9	6.6	6.1	20	24
F. nigra	81	2.9	1.1	1.8	0.8	3.0	2.6	4.8	5.6	243	389
Ostrya virginiana	41	4.5	1.5	3.7	1.2	11.6	7.2	28.0	21.0	476	1,148
Populus tremuloides	438	3.1	1.6	1.9	0.7	3.3	2.4	6.3	7.4	1445	2,759
Prunus pensylvanica	11	3.3	1.1	2.2	0.6	4.2	2.1	6.9	3.8	46	76
P. serotina	33	3.2	1.5	2.7	0.8	6.0	3.5	11.5	12.1	198	379
P. virginiana	8	2.1	0.5	1.4	0.3	1.7	0.8	1.8	0.8	14	14
Quercus rubra	4	3.0	0.3	1.7	0.8	2.7	2.1	4.1	3.3	11	16
Salix sp.	38	2.1	0.8	1.7	0.5	2.5	1.5	2.8	2.6	95	106
Tilia americana	23	3.4	1.4	2.5	0.7	5.3	3.0	10.1	8.5	122	232
Ulmus americana	5	4.7	1.6	4.0	0.8	13.0	5.2	32.7	21.3	65	163
Other species	6	1.8	1.2	1.3	0.5	1.5	1.5	2.1	3.7	9	13
Total (0.7854 ha)	1188									6537	14,506
Total per ha	1513									8323	18,470
Percent of growing space											11.2
Trees with dbh of 10.1 cm and larger											
Abies balsamea	9	10.9	3.9	4.4	1.0	16.0	7.2	98.0	69.8	144	882
Acer rubrum	130	7.9	2.2	4.8	1.3	19.8	13.0	81.2	61.2	2,574	10,556
A. saccharum	36	7.6	1.6	5.7	1.5	27.4	14.6	106.4	65.6	986	3,830
Amelanchier sp.											
Betula alleghaniensis	3	7.9	1.8	5.7	0.5	25.6	4.5	103.1	37.0	77	309
B. papyrifera	85	7.3	2.4	4.4	1.1	16.0	8.3	63.5	47.6	1,360	5,397
Fraxinus americana	2	9.6	4.2	5.8	1.8	27.2	16.0	147.5	134.3	54	295
F. nigra	45	5.3	1.9	3.0	0.8	7.5	4.3	21.9	19.2	338	986
Ostrya virginiana	9	6.9	1.3	5.2	1.5	22.5	12.8	80.6	50.1	202	725
Populus tremuloides	99§	8.3	2.1	4.6	1.3	17.7	10.0	78.8	56.8	1,752	7,801
Prunus pensylvanica											
P. serotina	21	4.7	1.1	4.5	1.7	17.9	15.0	45.1	44.0	376	947
P. virginiana											
Quercus rubra	13	9.5	2.5	7.7	2.8	52.3	34.9	273.8	233.3	680	3,559
Salix sp.											
Tilia americana	24	5.9	1.9	4.3	1.1	15.3	7.8	48.9	38.8	367	1,174
Ulmus americana	7	8.3	1.7	6.3	2.5	35.1	31.4	151.2	147.9	246	1,058
Other species	2	7.4	3.4	4.6	0.5	17.1	3.6	60.1	15.6	34	120
Total (0.7854 ha)	485									9,190	37,639
Total per ha	618									11,701	47,923
Percent of growing space											29.0

*Calculated: $(\text{crown width})^2 \times (\pi/4)$.
†Calculated: $(\text{crown width})^2 \times \text{crown length} \times (\pi/8)$.
‡Standard deviation.
§Includes two *Populus grandidentata* trees.

red and sugar maples), which accounted for almost three-fourths of all trees. When based on nuclear characteristics alone, the LD_{50} range seems to be too narrow to permit a reliable ranking of these four species according to their radiosensitivity. Improved results could be achieved by using tree or crown size, or some other physical characteristics of trees, along with the nuclear variable in predicting LD_{50}. Tree size or crown size has been correlated with radiation response in several studies but the results were contradictory. Woodwell and Rebuck (1967) and McCormick (1969) reported a negative correlation between tree size and radiosensitivity in several gymnosperms and angiosperms, but Miller (1968) observed a reversed trend for some of the same species. Perhaps this study will contribute to the understanding of these

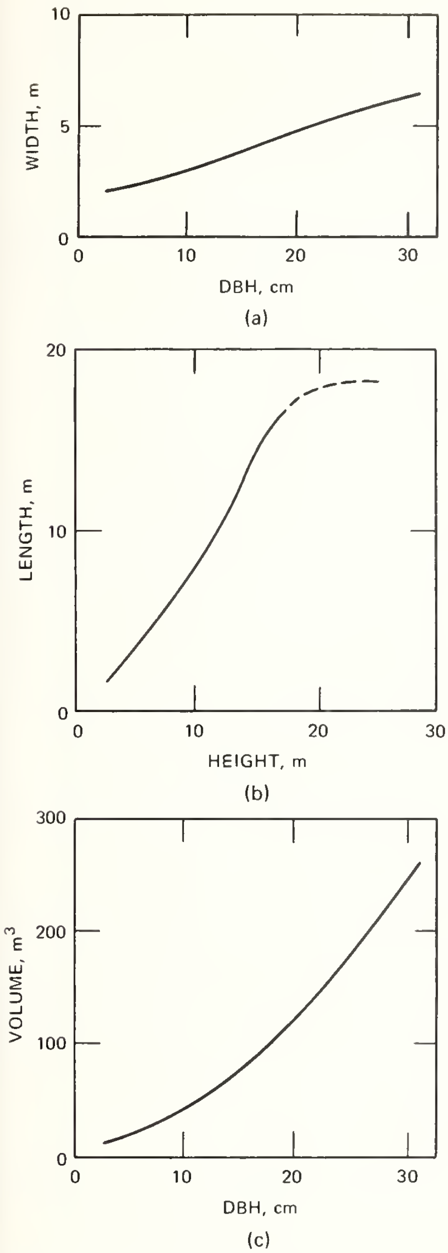


Fig. 14 Relation between dbh and crown width (a), height and crown length (b), and dbh and crown volume (c) of *Abies balsamea.*

(a) $Y = -0.64 + 8.21 \exp\left[-\frac{|(x/50) - 1|^2}{0.81}\right]$

$R^2 = 0.814$
SE = 0.56
N = 17

(b) $Y = -2.57 + 22.3 \exp\left[-\frac{|(x/25) - 1|^2}{0.49}\right]$

$R^2 = 0.956$
SE = 1.03
N = 15

(c) $Y = 7.22 + 339.5 \exp\left[-\frac{|(x/50) - 1|^3}{0.187}\right]$

$R^2 = 0.815$
SE = 24.6
N = 15

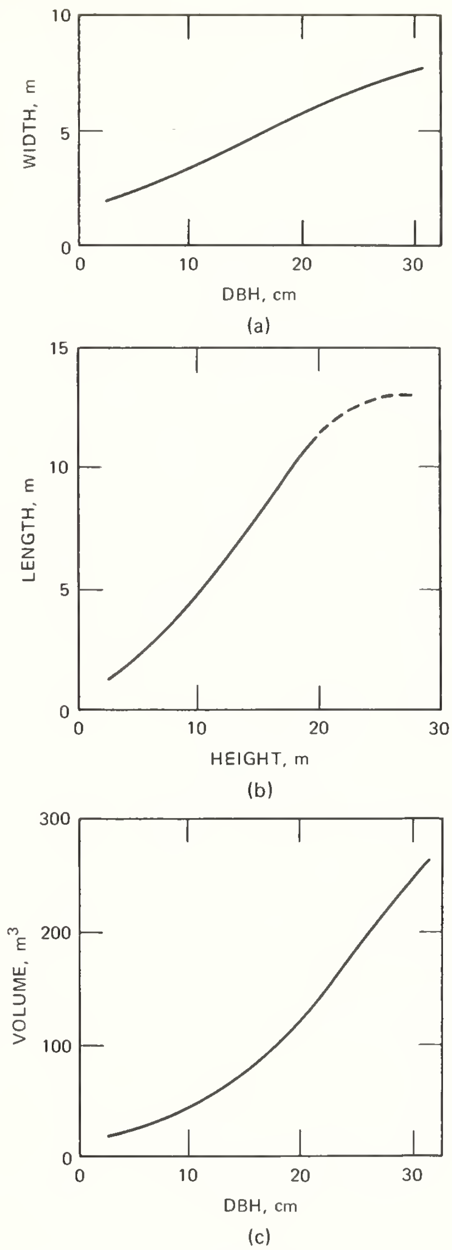


Fig. 15 Relation between dbh and crown width (a), height and crown length (b), and dbh and crown volume (c) of *Acer rubrum.*

(a) $Y = -1.12 + 10.17 \exp\left[-\frac{|(x/50) - 1|^{2.5}}{0.768}\right]$

$R^2 = 0.717$
SE = 0.95
N = 470

(b) $Y = 0.60 + 12.5 \exp\left[-\frac{|(x/25) - 1|^2}{0.336}\right]$

$R^2 = 0.768$
SE = 1.54
N = 465

(c) $Y = 20.3 + 321 \exp\left[-\frac{|(x/50) - 1|^3}{0.187}\right]$

$R^2 = 0.536$
SE = 42.5
N = 465

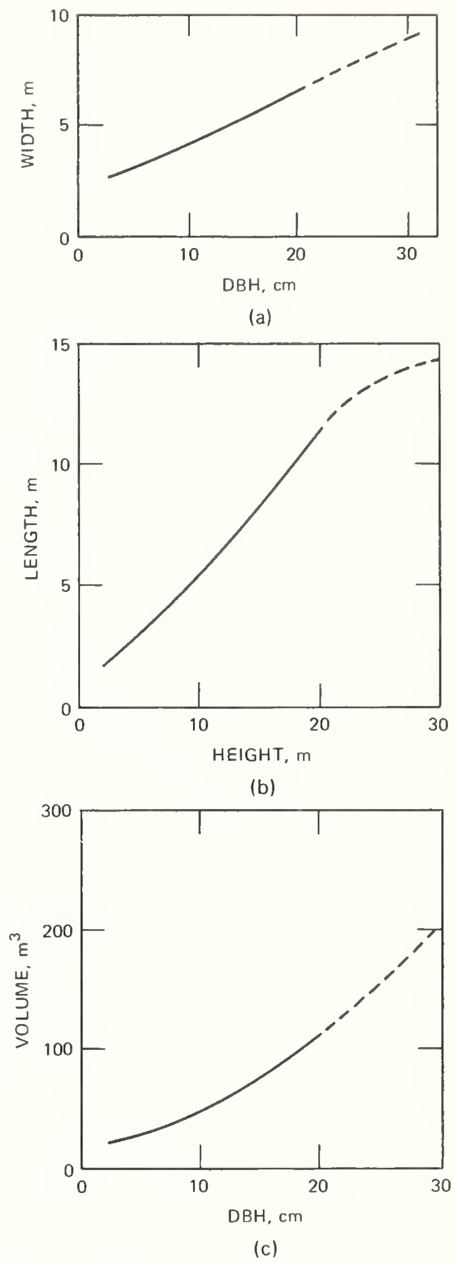


Fig. 16 Relation between dbh and crown width (a), height and crown length (b), and dbh and crown volume (c) of *Acer saccharum.*

(a) $Y = -1.31 + 12.86 \exp\left[-\frac{|(x/60) - 1|^{2.5}}{0.768}\right]$

$R^2 = 0.493$
SE = 1.31
N = 143

(b) $Y = -4.61 + 18.72 \exp\left[-\frac{|(x/27) - 1|^{1.5}}{0.784}\right]$

$R^2 = 0.668$
SE = 1.59
N = 143

(c) $Y = 13.0 + 298.6 \exp\left[-\frac{|(x/60) - 1|^3}{0.250}\right]$

$R^2 = 0.333$
SE = 37.4
N = 143

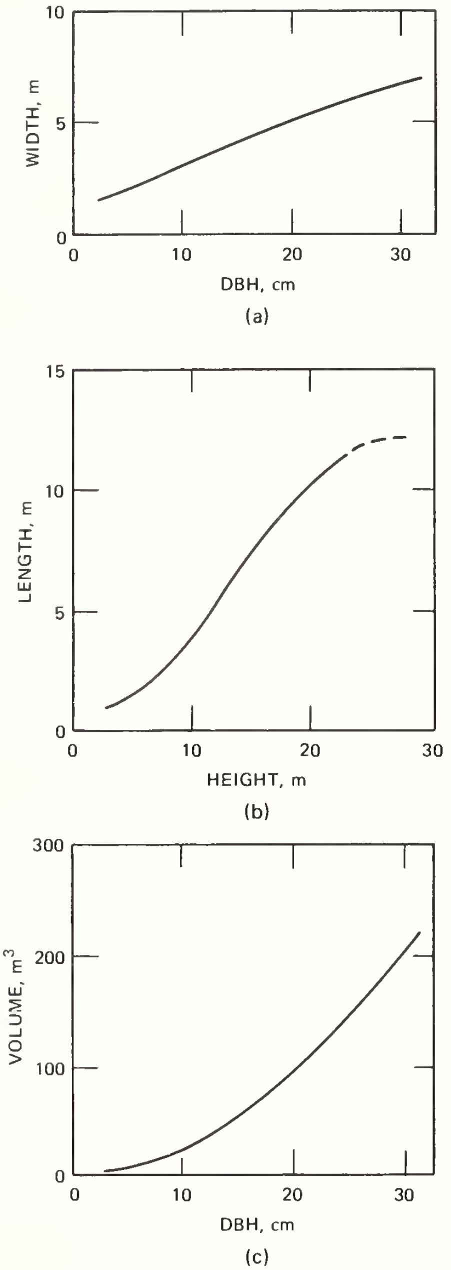


Fig. 17 Relation between dbh and crown width (a), height and crown length (b), and dbh and crown volume (c) of *Betula papyrifera.*

(a) $Y = -1.40 + 9.83 \exp\left[-\frac{|(x/50) - 1|^2}{0.846}\right]$

$R^2 = 0.750$
SE = 0.75
N = 159

(b) $Y = -1.76 + 14.0 \exp\left[-\frac{|(x/27) - 1|^{1.5}}{0.586}\right]$

$R^2 = 0.681$
SE = 1.74
N = 151

(c) $Y = 2.35 + 293.6 \exp\left[-\frac{|(x/50) - 1|^3}{0.166}\right]$

$R^2 = 0.686$
SE = 33.7
N = 151

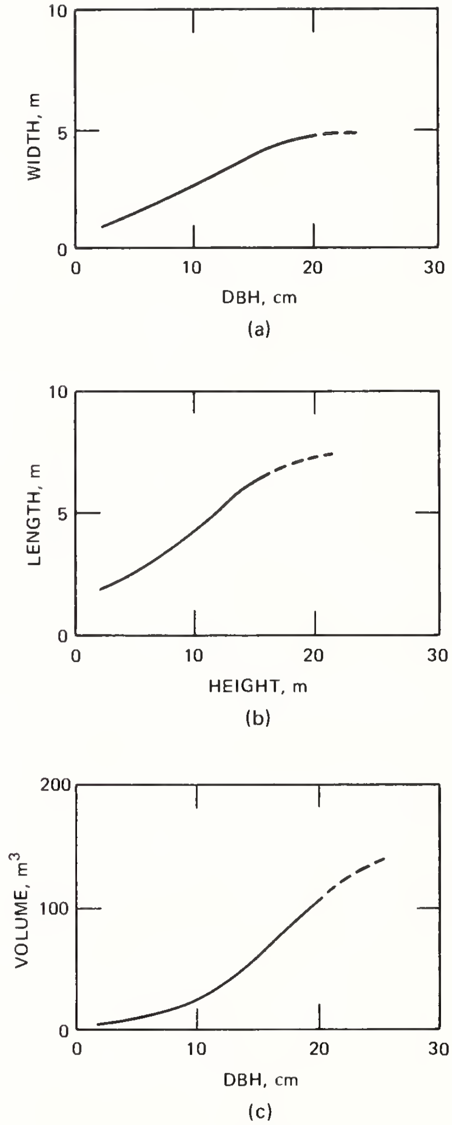


Fig. 18 Relation between dbh and crown width (a), height and crown length (b), and dbh and crown volume (c) of *Fraxinus nigra.*

(a) $Y = -0.72 + 6.44 \exp\left[-\frac{|(x/25) - 1|^{1.5}}{0.689}\right]$

$R^2 = 0.659$
SE = 0.79
N = 119

(b) $Y = -0.53 + 7.83 \exp\left[-\frac{|(x/20) - 1|^{1.5}}{0.716}\right]$

$R^2 = 0.521$
SE = 1.23
N = 107

(c) $Y = 9.78 + 125.9 \exp\left[-\frac{|(x/25) - 1|^2}{0.16}\right]$

$R^2 = 0.552$
SE = 16.1
N = 106

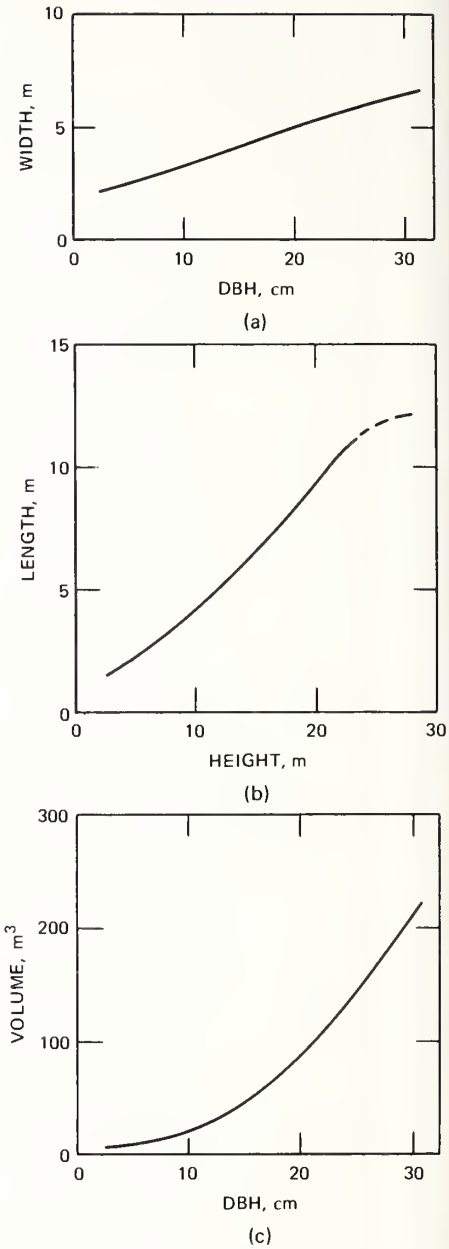


Fig. 19 Relation between dbh and crown width (a), height and crown length (b), and dbh and crown volume (c) of *Populus tremuloides.*

(a) $Y = -1.38 + 9.36 \exp\left[-\frac{|(x/50) - 1|^{2.5}}{0.768}\right]$

$R^2 = 0.883$
SE = 0.64
N = 504

(b) $Y = -2.47 + 16.2 \exp\left[-\frac{|(x/27) - 1|^{1.5}}{0.586}\right]$

$R^2 = 0.904$
SE = 1.08
N = 495

(c) $Y = -17.9 + 371.9 \exp\left[-\frac{|(x/50) - 1|^2}{0.302}\right]$

$R^2 = 0.787$
SE = 30.2
N = 491

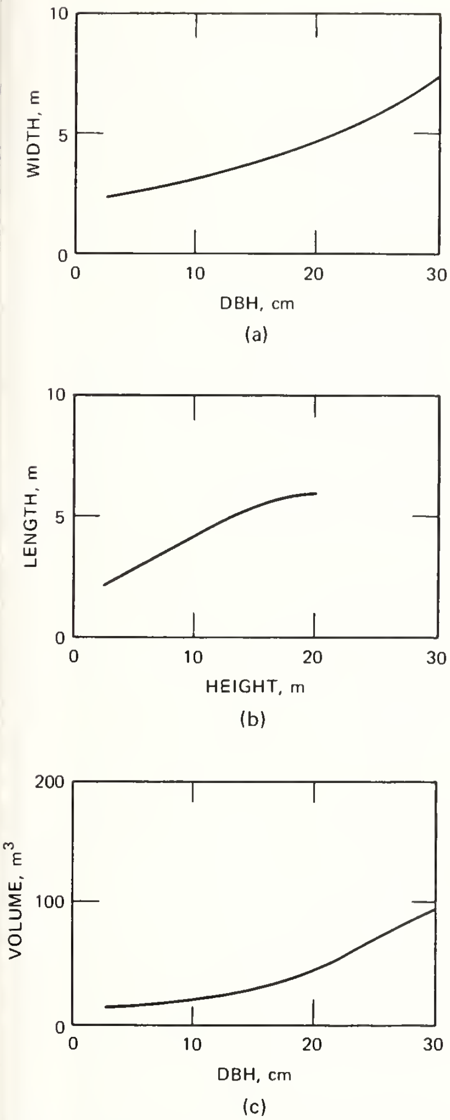


Fig. 20 Relation between dbh and crown width (a), height and crown length (b), and dbh and crown volume (c) of *Prunus serotina*.

(a) $Y = 0.216 + 6.39 \exp\left[-\frac{|(x/40) - 1|^{1.8}}{0.794}\right]$

$R^2 = 0.491$
SE = 1.06
N = 44

(b) $Y = -0.205 + 6.07 \exp\left[-\frac{|(x/21) - 1|^{2}}{0.81}\right]$

$R^2 = 0.544$
SE = 1.08
N = 42

(c) $Y = 10.96 + 116.6 \exp\left[-\frac{|(x/40) - 1|^{2}}{0.187}\right]$

$R^2 = 0.342$
SE = 27.9
N = 41

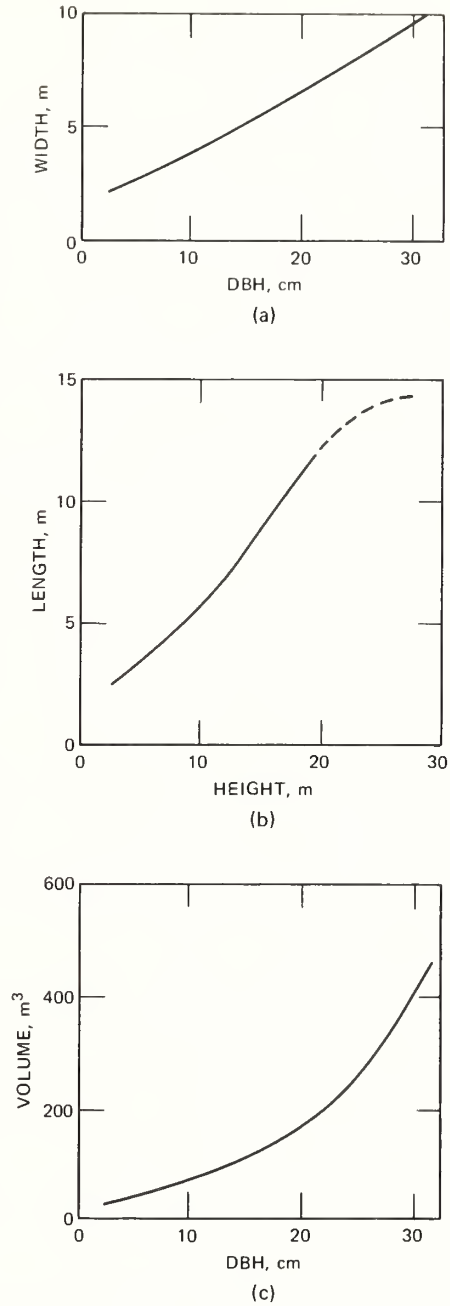


Fig. 21 Relation between dbh and crown width (a), height and crown length (b), and dbh and crown volume (c) of *Quercus rubra*.

(a) $Y = -2.73 + 17.09 \exp\left[-\frac{|(x/60) - 1|^{2}}{0.723}\right]$

$R^2 = 0.678$
SE = 1.79
N = 22

(b) $Y = -0.90 + 15.16 \exp\left[-\frac{|(x/25) - 1|^{1.5}}{0.561}\right]$

$R^2 = 0.727$
SE = 1.74
N = 21

(c) $Y = 40.56 + 818.9 \exp\left[-\frac{|(x/60) - 1|^{3}}{0.157}\right]$

$R^2 = 0.515$
SE = 151.7
N = 21

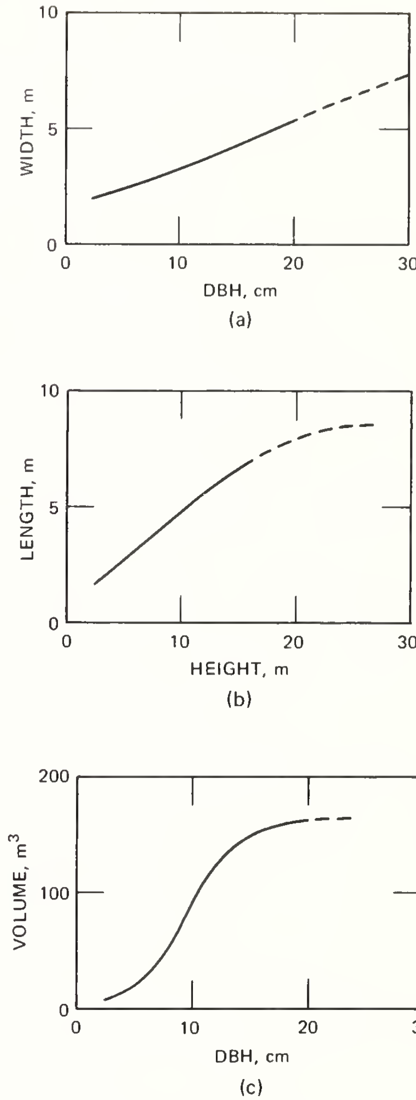


Fig. 22 Relation between dbh and crown width (a), height and crown length (b), and dbh and crown volume (c) of *Tilia americana*.

(a) $Y = 0.516 + 7.66 \exp\left[-\frac{|(x/50) - 1|^{3}}{0.512}\right]$

$R^2 = 0.692$
SE = 0.71
N = 39

(b) $Y = -1.35 + 9.81 \exp\left[-\frac{|(x/27) - 1|^{2.5}}{0.666}\right]$

$R^2 = 0.552$
SE = 1.35
N = 36

(c) $Y = 7.10 + 155.0 \exp\left[-\frac{|(x/50) - 1|^{6}}{0.0989}\right]$

$R^2 = 0.716$
SE = 18.8
N = 36

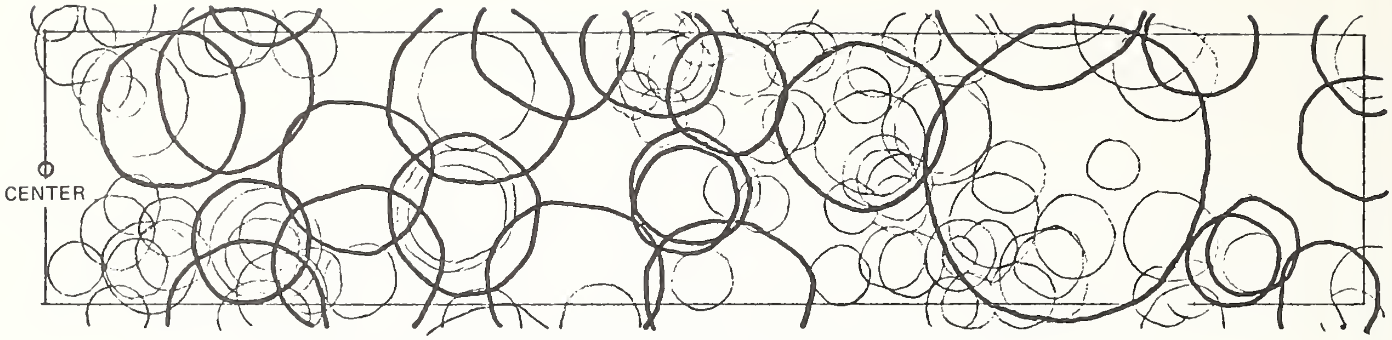


Fig. 23 Vertical projection of crowns in a 10-m wide strip from the site center to a 50-m distance along northern hardwood transect 1. Main canopy trees are shown in heavy line.

controversial relationships and develop a better method for predicting LD_{50}.

The information summarized in this chapter is intended primarily for radioecological purposes, but a part of it also has general ecological and forestry usefulness. A close examination of the age distribution of all species, particularly of the quaking aspen, indicated that in the last 50 years the experimental area was disturbed several times by logging, road building, and perhaps also by fire. The most recent disturbance occurred less than 10 years ago.

Total crown projection area of trees within 50 m from the site center was computed assuming that crowns were circular in horizontal cross section. The overlapping crowns covered a cumulative area of about 2 hectares per hectare of land (ha/ha); trees larger than 10 cm in dbh accounted for 1.17 ha/ha, and smaller trees, for about 0.83 ha/ha (Table 5). No correction was made for the area occupied by a logging road (about 5%) or for other open spaces within the area. Vertical crown projection of a 10-m-wide and 50-m-long transect is shown in Fig. 23. For mixed hardwood and oak–hickory stands of southern Illinois, Minckler and Gingrich (1970) reported that the projected crown areas of trees larger than 4.6 in. (11.7 cm) in dbh ranged from 1.12 to 1.40 ha/ha. In a tropical rain forest of Puerto Rico, the total projected crown area of all trees taller than 5 m was estimated at 2.33 ha/ha (from the data of Addor, Rushing, and Grabau, 1970). Crown projection area in 25 western Oregon red alder stands 4 to 45 years old ranged from 4.19 ha/ha in a 4-year-old dense stand to 0.92 ha/ha in the oldest 45-year-old open-grown stand (Zavitkovski, unpublished).

Total growing space enclosed by the main canopy (average height 16.5 m) in stands within 50 m from the site center was estimated at 165,000 m^3/ha. About 29% of that space was occupied by crowns of the main canopy (trees larger than 10 cm in dbh); crowns of smaller trees filled an additional 11% of the space. Stems occupied only a small space, tentatively estimated at 81 m^3/ha or less than 0.05% of the total. Space filled by crowns of shrubs was probably less than 5% and ground vegetation occupied less than 2% of the total. We found no comparable data in the literature. In the red alder stands mentioned previously, the proportion of the total growing space occupied by crowns ranged from about 85% in a 4-year-old stand to about 10.7% in the 45-year-old stand and averaged about 25% for all 25 stands included in the study.

Productivity of forest communities is often expressed as a site index determined from the dominant trees of the main stratum. The site index of 67 ft (about 20.5 m) for 50-year-old aspen in the radiation forest is high in comparison to Gevorkiantz's data (1956) for aspen in the lake states. Paper birch ranks intermediate with a site index of 64 ft (19.5 m) when compared with other paper birch stands in northern Wisconsin (Cooley, 1962). Biomass of the stands within 50 m from the site center estimated from their average height (about 16 m) is about 150 tonnes/ha (Zavitkovski and Stevens, 1972). Based on these data, it can be concluded that the productivity of the sampled forest communities is typical for northern Wisconsin.

Table 6

RELATIONSHIPS BETWEEN TREE AND CROWN DIMENSIONS*

	Crown width, m, for indicated dbh				Crown length, m, for indicated height			Crown volume, m^3, for indicated dbh			
	dbh, cm				height, m			dbh, cm			
Species	5	10	20	30	5	10	20	5	10	20	30
Abies balsamea	2.4	3.1	4.6	6.1	3.5	8.1	18.0	14	29	114	248
Acer rubrum	2.6	3.7	6.0	7.8	2.5	4.9	11.7	27	41	121	248
A. saccharum	3.2	4.3	6.7		2.7	5.3	11.2	27	42	104	
Betula papyrifera	2.4	3.2	5:0	6.7	2.2	4.2	9.4	5	11	55	134
Fraxinus nigra	1.6	2.6	4.9		2.6	4.2	7.3	12	23	108	
Populus tremuloides	2.1	3.1	5.1	6.8	2.2	4.4	10.5	8	27	95	201
Prunus serotina	2.6	3.2	4.7	6.0	2.8	4.1	5.8	13	17	42	94
Quercus rubra	2.6	3.8	6.5	9.4	3.3	5.7	12.0	47	61	165	410
Tilia americana	2.4	3.3	5.5		2.6	4.8	8.0	8	18	104	

*Adapted from Figs. 14-22 for selected dbh and height values.

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Properties of the Tree Flora in the Forest Transition from Aspen to Maple–Birch Type

8

PETER G. MURPHY and REBECCA R. SHARITZ†*

*Michigan State University, East Lansing, Michigan, and †Savannah River Ecology Laboratory, Aiken, South Carolina

ABSTRACT

Five belt transects were used to study certain properties of the tree flora in a zone of transition between an aspen-dominated area and a maple–birch-dominated area in the Enterprise Radiation Forest. The properties studied included tree-species composition of the canopy, sapling, and seedling strata; population densities; species importance values; species diversity; and leaf-area index.

On the basis of known ecological characteristics of the dominant species, leaf-area index, species diversity, and an analysis of similarity between canopy and understory tree-species composition, the ecotone appears to include forest types representing three stages of maturity, from the least mature aspen area to the most mature, although still successional, maple–birch area. Because of a complicated and undocumented history of disturbance in the area, the ecotone is not assumed to represent a typical forest sere for undisturbed succession at the Enterprise site.

It is predicted that the aspen area will experience the greatest aboveground tree mortality in response to chronic gamma irradiation but that this area will also be the quickest to recover to an approximate preirradiation condition. The extent of tree mortality in the intermediate segment of the transition zone and in the maple–birch area is expected to be somewhat less than that in the aspen area. The overall ecological effect in all areas along the transition will be a setback in successional status, which will be evidenced by changes in the parameters documented in this study. Long-term recovery rates will depend in large part on the extent of competition between tree sprouts, seedlings, and shrubs under the opened canopy.

The upland conifer–hardwood forest of northern Wisconsin has been described as a continuum lacking compositionally discrete communities (Brown and Curtis, 1952). In disturbed areas, however, gradients in floristic composition may be relatively abrupt and pronounced, and the forest can best be described as a mosaic of floristically distinguishable forest types. Such is the case throughout much of our northern deciduous forest, including the Enterprise Radiation Forest. Here lumbering has altered the original forest composition and replaced a more homogeneous forest with a patchwork of forest types representing various stages of secondary succession.

Coupling the various recognizable forest types in the mosaic pattern are abrupt zones of transition called ecotones. The areal coverage of the ecotones is often considerable; their linear extent at the Enterprise site was estimated to be 243 m/ha, based on measurements from a Forest Service map of forest types in the area (see Fig. 2, Chap. 1, this volume). The width of these zones can be defined only arbitrarily, but, if the average width were considered to be 10 m, the area occupied by abrupt ecotones would be about 25% of the total forest area in the vicinity of the Enterprise site. Thus disturbance-induced forest ecotones may constitute a spatially significant part of the forest ecosystem, and data concerning their compositional characteristics and response to radiation are desirable.

None of the forest irradiation studies undertaken previously have intentionally dealt with ecotones. The tendency has been to study floristically homogeneous sites. The geometry of the radiation field at the Enterprise site offers a unique opportunity for the study of stressed forest ecotones, however, because of the placement of the radiation source at the confluence of three different forest types.

In this chapter we describe compositional characteristics of the tree flora along the forest transition from aspen forest type to a maple–birch-dominated forest. The problem of defining the forest types composing the experimental site is described in depth by Zavitkovski in Chap. 6, this volume. As used here the term "ecotone" applies to the entire transition, with aspen and maple–birch forest types representing the end points. The term "midecotone" refers to the area between the aspen and maple–birch end points. This ecotone was selected for study because it couples forest types of distinctly different successional status. Our primary objective is to describe the preirradiation characteristics of specific portions of this forest ecotone in terms of such floristic properties as canopy-, sapling-, and seedling-strata composition and tree-species diversity. The values obtained for certain floristic parameters of the aspen and maple–birch forest types at the ends of the ecotone differ from those reported in Chap. 6. Our values are based only on vegetation included within the terminal portions of the ecotone gradient, whereas Zavitkovski's values are based on analysis of a larger portion of a more homogeneous forest. The data reported here were obtained from permanently marked sampling plots and will be used as a base line for determining radiation effects in these plots.

METHODS

Belt transects 2 m wide were established concentric to the radiation source at 10, 20, 30, 40, and 50 m from the source (Fig. 1). For sampling purposes the transects were sectioned into increments of 5 m as shown in the figure. The transects extended from inside the maple–birch forest type to inside the aspen forest type. Radial transects established by resident personnel for sampling in the aspen and maple–birch forest types marked the end points of the ecotone transects. In this preirradiation study sample plots were grouped for analysis within each of the three main ecotone sectors (i.e., aspen, midecotone, maple–birch). The same plots will be used in postirradiation studies, but the plots from different positions along the radiation gradient will not be grouped. To compute species-diversity values, which are known to be area dependent, we selected an equal number of plots (11) from each sector. All other calculations are based on 11 plots in the aspen area, 16 in the midecotone, and 24 in the maple–birch area. The number of plots in each area differed because of differences in size of the areas available for sampling.

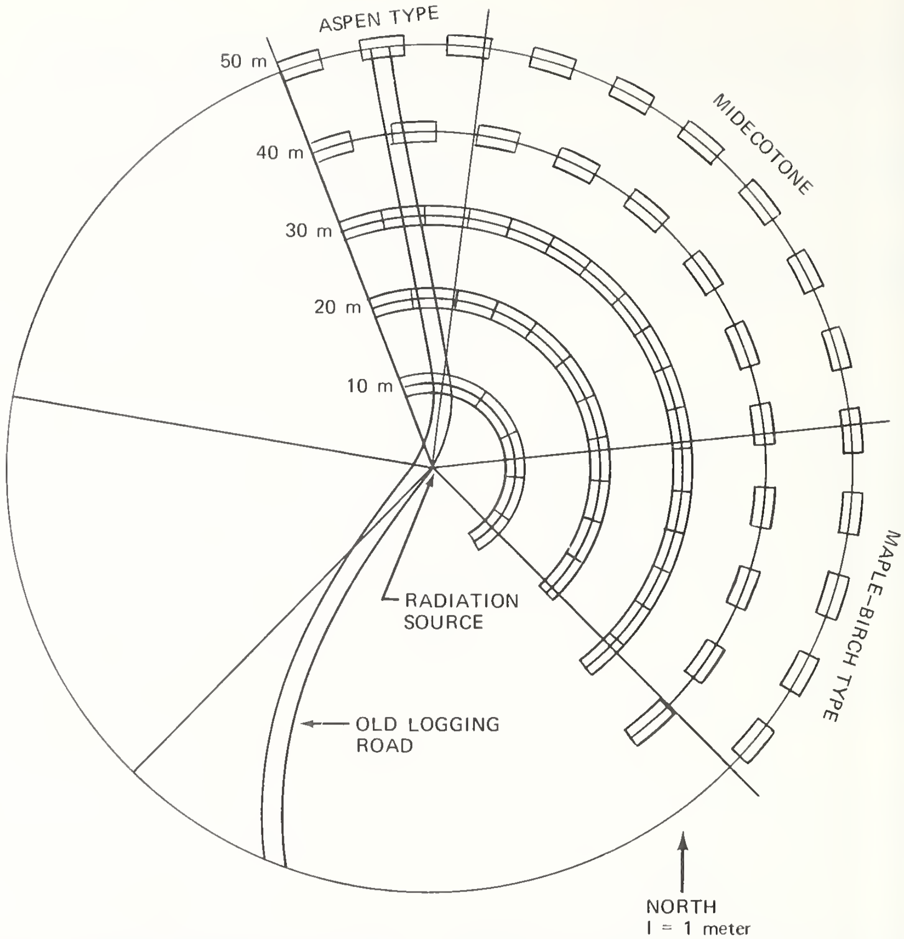

Fig. 1 Enterprise Radiation Forest, site 1. Diagram shows relative locations of aspen and maple–birch forest types with intervening transitional area (midecotone). Five concentric transects and sampling plots are also shown. The six radial transects were established by resident personnel.

Leaf-litter samples were obtained from 20 0.5-m-square quadrats in each ecotone sector immediately following leaf fall (Oct. 30, 1971). We avoided areas immediately adjacent to the logging road when placing quadrats. All leaves produced during the 1971 growing season, except those from the herbaceous ground flora, were collected from each quadrat to estimate the ratio of single-surface leaf area to ground-surface area (leaf-area index, LAI). A relation between dry leaf weight and leaf area was established for each of the three ecotone sectors. The percentage of error was determined by comparing the estimated LAI with actual measurements of leaf area. Estimated values based on 25 samples containing 20 leaves each proved too low by 13.4% (standard error, ±1.6%). All reported values of LAI were corrected by this amount.

RESULTS

Species–Area Relations

The curves in Fig. 2 show the relation between number of species tallied and cumulative area sampled in the three ecotone sectors. To obtain the curves, we selected 11 quadrats in random order from each area. No new canopy-size or seedling-size tree species were encountered as total sample area increased above 90 m^2 in any of the three areas. This is also true of sapling-size tree species, except in the aspen area, in which the curve at 110 m^2 (total sample) still had not leveled off. Several unrecorded tree species were present in the unsampled areas between transects and between plots. In this study canopy trees are considered to have a diameter at breast height (dbh) of at least 2.5 cm, saplings are considered to be 30 cm or more in height with a dbh of less than 2.5 cm, and seedlings are considered to be less than 30 cm in height.

Tree-Species Composition

The absolute densities (individuals per 10 m^2) of canopy trees, saplings, and seedlings are shown in Table 1. The midecotone has the lowest density in all three strata, and the aspen area is most densely populated in all three strata. The midecotone and aspen-area densities differ significantly at the 5% level in the canopy, sapling, and seedling strata. Neither the midecotone nor the aspen-area canopy or seedling densities differ from the maple–birch area densities at the 5% level of significance. Sapling densities are significantly different at the 5% level in each of the three areas. In all three areas seedlings constitute more than 50% of total tree-species density (Fig. 3).

Table 2 contains relative densities of tree species in the canopy and understory strata of the three areas (only species with relative densities of at least 10% are identified).

Importance values (Curtis and McIntosh, 1950) incorporate relative frequency and relative dominance as well as relative density. These values, which attain a maximum of 300 for a species in monoculture, give a better indication of the prominence of a species in a community than does relative density alone

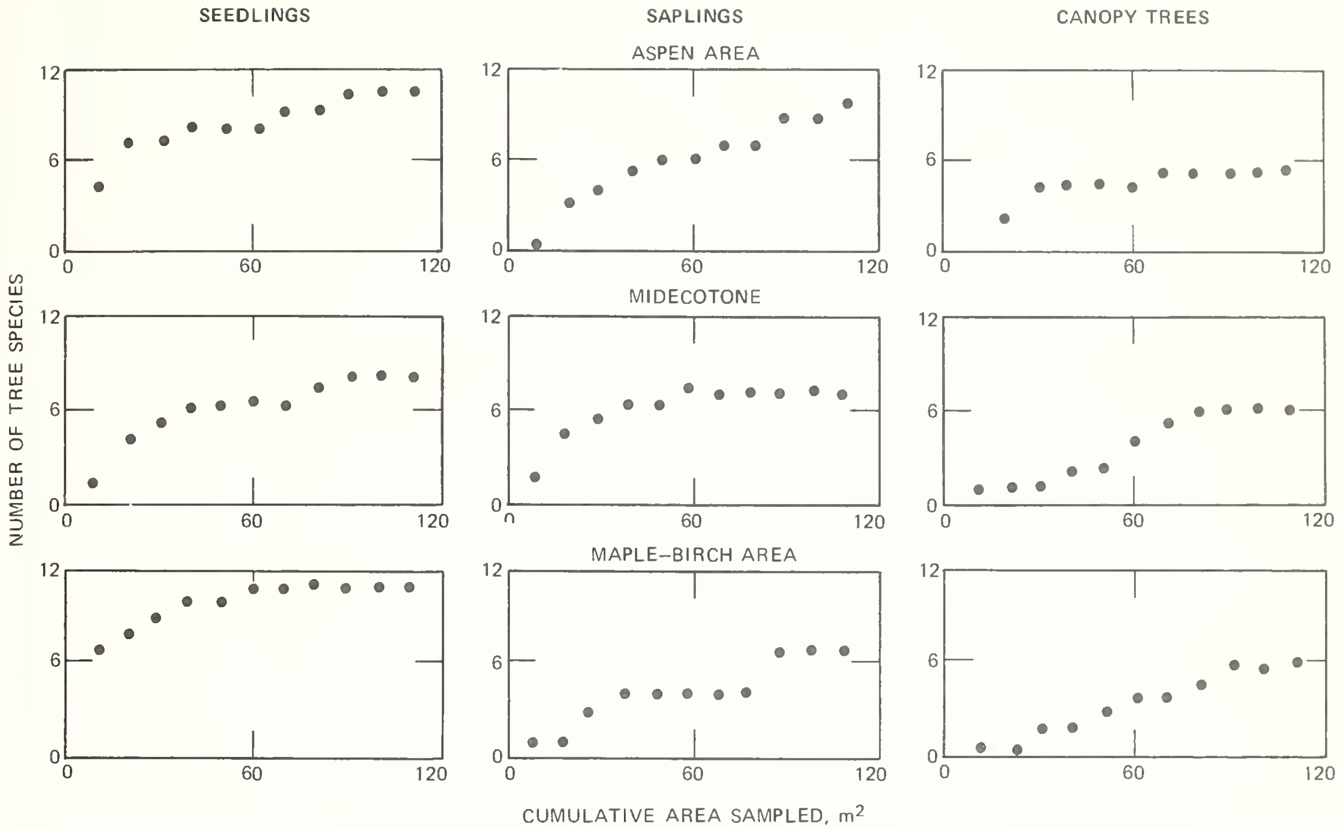

Fig. 2 Relation of number of tree species tallied to cumulative area sampled.

Table 1

ABSOLUTE DENSITIES OF TREE SPECIES OF THE CANOPY AND UNDERSTORY STRATA

Stratum	Density, number of individuals per 10 m^2 ± 1 SE*		
	Aspen area	Midecotone	Maple–birch area
Canopy	3.45 ± 0.76	1.68 ± 0.32	2.12 ± 0.35
Sapling	6.34 ± 0.12	1.22 ± 0.02	2.23 ± 0.03
Seedling	13.09 ± 2.27	6.06 ± 1.46	9.33 ± 1.65

*Standard error.

Table 3 indicates that ranking of importance values for the midecotone species parallels ranking by relative densities, with *Populus tremuloides, Acer saccharum, Prunus serotina,* and *A. rubrum* being the four most important canopy species. Importance values were not computed for saplings or seedlings.

In the aspen area *P. tremuloides* accounts for 68.4% and *A. rubrum* for 18.4% of the canopy trees (Table 2). The importance values of the two species are 178.3 and 59.5, respectively. In the sapling stratum *Amelanchier* sp. is most abundant, followed by *P. tremuloides* and *Prunus serotina. Acer rubrum* has the highest relative density in the seedling stratum (28.5%), whereas *P. tremuloides* has a relative density of only 1.4%.

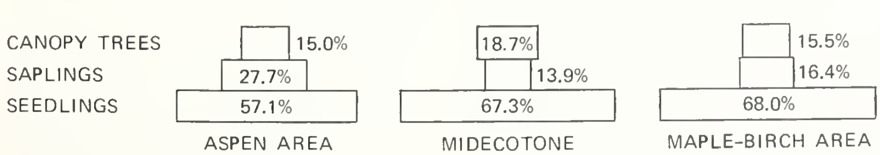

Fig. 3 Size class distribution of tree species. Values are percent of individuals.

In the maple–birch canopy, *A. rubrum, Betula papyrifera,* and *A. saccharum,* the three most abundant species, also have the highest importance values. *Acer saccharum, Fraxinus nigra, Amelanchier* sp., and *P. serotina* lead in relative density in the sapling stratum. The seedling stratum is dominated in numbers by *A. saccharum*, which has a relative density of 31.2%, whereas *A. rubrum,* the canopy dominant, has a relative density of only 7.1% in the seedling stratum.

Diversity of Tree Species

The sampled plots of the midecotone canopy contain six species; the aspen canopy, five; and the maple–birch canopy, six. (A complete inventory of canopy trees within the 50-m circle can be found in Chap. 6.) In a consideration of diversity, if equitability of relative densities is taken into account, the diversities of the three canopies are not as close as the similaiity in numbers of species would indicate (Table 4). The Shannon–Weaver diversity index (ID) (Margalef, 1958) was used because it incorporates both equitability and variety in a single index value. The evenness index (E) (Pielou, 1969) indicates the extent to

Table 2

RELATIVE DENSITIES OF TREE SPECIES OF THE CANOPY AND UNDERSTORY STRATA

Aspen area		Midecotone		Maple–birch area	
Species	Relative density, %	Species	Relative density, %	Species	Relative density, %
		Canopy			
Populus tremuloides	68.4	*Populus tremuloides*	37.0	*Acer rubrum*	37.2
Acer rubrum	18.4	*Acer saccharum*	18.5	*Betula papyrifera*	19.6
Other (3 species)	13.2	*Prunus serotina*	14.8	*Acer saccharum*	11.8
		Acer rubrum	14.8	Other (7 species)	31.4
		Tilia americana	11.1		
		Other (1 species)	3.8		
		Saplings			
Amelanchier sp.	42.4	*Acer rubrum*	26.3	*Acer saccharum*	24.5
Populus tremuloides	18.2	*Prunus serotina*	21.0	*Fraxinus nigra*	22.6
Prunus serotina	16.7	*Acer saccharum*	10.5	*Amelanchier* sp.	20.8
Other (6 species)	22.7	*Amelanchier* sp.	10.5	*Prunus serotina*	15.1
		Other (6 species)	31.7	Other (5 species)	17.0
		Seedlings			
Acer rubrum	28.5	*Abies balsamea*	54.6	*Acer saccharum*	31.2
Amelanchier sp.	17.4	*Acer saccharum*	17.5	*Abies balsamea*	17.0
Prunus serotina	17.4	*Acer rubrum*	14.4	*Prunus serotina*	14.3
Abies balsamea	16.0	Other (5 species)	13.5	*Amelanchier* sp.	12.5
Other (6 species)	20.7			Other (8 species)	25.0

Table 3

IMPORTANCE VALUES* OF CANOPY TREES

Aspen area		Midecotone		Maple–birch area	
Species	IV	Species	IV	Species	IV
Populus tremuloides	178.3	*Populus tremuloides*	90.4	*Acer rubrum*	102.1
Acer rubrum	59.5	*Acer saccharum*	64.9	*Betula papyrifera*	72.1
Betula papyrifera	30.1	*Prunus serotina*	48.9	*Acer saccharum*	36.0
Fraxinus nigra	21.8	*Acer rubrum*	46.8	*Prunus serotina*	23.2
Acer saccharum	10.3	*Tilia americana*	28.4	*Salix* sp.	15.1
		Abies balsamea	20.8	*Ostrya virginiana*	13.7
				Quercus rubra	13.6
				Populus tremuloides	8.6
				Ulmus americana	8.6
				Fraxinus nigra	7.4

*Importance value (IV) is relative density + relative frequency + relative dominance, where dominance is basal area (see Curtis and McIntosh, 1950).

which relative densities vary between species. Species arrays in which each species has the same relative density have an E value of 1.0; arrays with unequal relative densities (i.e., less diverse) have values less than 1.0.

The ID of 2.08 and the E of 0.81 in the midecotone canopy are intermediate to the values for the aspen and maple–birch canopies (Table 4). The aspen canopy has the lowest ID, and the maple–birch canopy has the highest. The E value, which ranges from 0.61 in the aspen area to 0.98 in the maple–birch area, indicates that the differences in ID are due largely to differences in equitability. Diversity relations in the sapling and seedling strata do not parallel those in the canopy stratum (Table 4). The midecotone, for example, has the highest sapling diversity but the lowest seedling diversity.

Leaf-Area Index (LAI)

Single-surface LAI for trees and shrubs in the midecotone was 4.7 (Fig. 4). This value is intermediate to the aspen-area LAI (3.9) and the maple–birch-area LAI (5.5) but is not significantly different from either at the 5% level. However, the aspen and maple–birch values differ significantly from each other at the 1% level.

DISCUSSION

The Ecotone as a Gradient of Forest Maturity

Perturbations as diverse in character as fire, pollution, and ionizing radiation have been shown to have similar effects on the structure of plant communities (Odum, 1965, and Woodwell, 1970). The

Table 4

DIVERSITY OF TREE SPECIES BASED ON A TOTAL SAMPLE SIZE OF $110\ m^2$ IN EACH AREA

Index	Aspen area	Mid-ecotone	Maple–birch area
		Canopy	
No. of species	5	6	6
ID*	1.41	2.08	2.53
E†	0.61	0.81	0.98
		Saplings	
No. of species	10	7	7
ID*	2.58	2.72	2.37
E†	0.78	0.97	0.84
		Seedlings	
No. of species	10	8	11
ID*	2.76	1.93	2.68
E†	0.83	0.64	0.78

*ID (Shannon–Weaver index of diversity) = $-\Sigma p_i \log_2 p_i$, where p_i is the decimal fraction of total individuals belonging to the *ith* species (see Margalef, 1958).

†E (evenness index) = $\mathrm{ID}/\log_2$ (number of species) (see Pielou, 1969).

Table 5

SIMILARITY OF TREE SPECIES COMPOSITION BETWEEN STRATA WITHIN EACH AREA

	SC*		
Area	Seedlings/saplings	Seedlings/canopy	Saplings/canopy
Aspen	0.80	0.53	0.40
Midecotone	0.67	0.57	0.59
Maple–birch	0.73	0.62	0.60

*SC (similarity coefficient) = $2c/(a + b)$, where the two units being compared contain a and b numbers of species, respectively, and have c number of species in common (see Greig-Smith, 1964).

overall effect of stress is inevitably a setback to an earlier successional stage, i.e., to a state of reduced maturity. The setback is usually evidenced by changes in species composition and diversity. The ecotone from aspen to maple–birch forest type studied in this investigation represents a gradient of forest maturity from early forest succession to intermediate forest succession. Although detailed records of the disturbance are not available, the existence of the successional forest can be attributed to lumbering and related disturbance in the recent past. Our discussion concerns the various states of maturity along the ecotone gradient. We have attempted to predict the pattern of change that can be expected along the ecotone as the forest restructures in response to ionizing radiation stress.

The aspen area represents the least mature segment of the ecotone. *Populus tremuloides*, a short-lived species that often becomes dominant after a fire or other disturbance, is presently the dominant canopy species, having a relative density of 68.4% (Table 2) and an importance value of 178.3 (Table 3). The area is still in an early state of recovery and most of the trees are less than 20 years of age (Chap. 13, this volume). The similarity coefficients (SC) (Greig-Smith, 1964) shown in Table 5 indicate that the sapling and seedling strata are floristically more similar to each other (0.80) than either is to the canopy stratum (0.40 and 0.53, respectively). (A value of 1.0 would indicate complete similarity in terms of species shared.) This suggests that the forest composition is changing. As is typical of successional forests, the seedling stratum is dominated by species characteristic of later successional stages, including *A. rubrum*, *Amelanchier* sp., and *P. serotina*. The relative density of the canopy dominant, *P. tremuloides*, is 18.2% in the sapling stratum and only 1.4% in the seedling stratum.

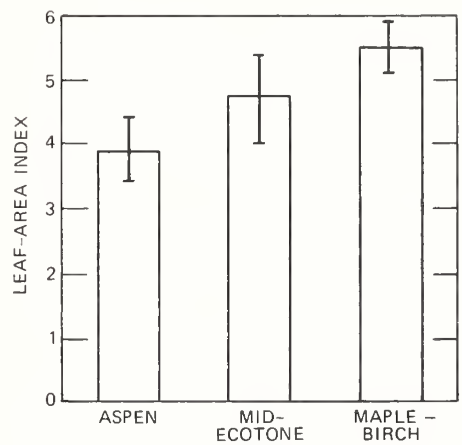

Fig. 4 Single-surface leaf-area index in the three forest areas ±2 standard errors of the mean.

The canopies of northern Wisconsin climax or near-climax forests on favorable sites are dominated by *A. saccharum*. Brown and Curtis (1952) reported an average importance value of 145 for *A. saccharum* in such stands. In this study the maple–birch area represents the mature end of the ecotone gradient, but it is definitely preclimax in character. Presently *A. saccharum* has a relative density in the canopy of only 11.8% (Table 2) and an importance value of only 36.0 (Table 3). The present dominants are *A. rubrum* and *B. papyrifera*, which together account for 56.8% of the canopy species and have importance values of 102.1 and 72.1, respectively. The species are typical canopy dominants in preclimax forests (Brown and Curtis, 1952). The early successional *P. tremuloides* is also present in the maple–birch area (importance value, 8.6). In both the sampling and seedling strata, *A. saccharum* leads in relative density (24.5 and 31.2%, respectively). Both *A. rubrum* and *B. papyrifera* are important in the canopy, but in the sapling stratum *A. rubrum* has a relative density of only 1.8%, and *B. papyrifera* is absent from sampled plots. In the seedling stratum the relative densities of *A. rubrum* and *B. papyrifera* are 7.1 and 0.4%, respectively. There is greater similarity between the sapling and seedling strata (SC, 0.73) than there is between either of these two strata and the canopy (0.60 and 0.62, respectively). The canopy and understory strata can be expected to increase in similarity as the more successional canopy species are eliminated by the increasing dominance of *A. saccharum*. In a steady-state (climax) forest, the similarity coefficient for tree species of canopy and understory should approach a value of 1.0, indicating near complete floristic similarity between strata.

The midecotone canopy is of intermediate maturity and contains species characteristic of the adjacent aspen and maple–birch areas. Of the six species present in the canopy, *P. tremuloides* leads in importance value, followed by *A. saccharum*, *P. serotina*, and *A. rubrum* (Table 3). These four species also exhibit the highest relative densities in the can-

opy. In the sapling stratum the highest relative densities are attained by *A. rubrum, P. serotina, A. saccharum,* and *Amelanchier* sp. (Table 2). The seedling stratum contains a high percentage of *Abies balsamea,* followed by *Acer saccharum* and *A. rubrum* (Table 2). No *P. tremuloides* seedlings were found within the sampled plots. Most of the *A. balsamea* seedlings will probably be eliminated as the undisturbed canopy closes because the species "does not thrive in the dense shade cast by more mesic stands of *A. saccharum* which usually replace it" (Brown and Curtis, 1952). As in the aspen and maple–birch areas, the SC values in Table 5 indicate that the sapling and seedling strata are floristically more similar to each other than either is to the canopy stratum. The floristic similarity between understory strata and the canopy stratum is intermediate to that found in the aspen and maple–birch areas.

Similarity coefficients indicate that, in terms of canopy species shared among areas along the ecotone, the midecotone is almost equally similar to both the aspen and maple–birch areas (Table 6). The SC values for sapling- and seedling-stratum comparisons among areas were relatively high, ranging from 0.70 to 0.82; this indicates more similarity in the regenerative zone throughout the three areas than in the canopy stratum. The large number of seedlings relative to canopy trees (Fig. 3) indicates potential for compositional change in all three areas, and the trend toward a more homogeneous forest than presently exists is apparent.

Both the ID and E values of the canopy of the midecotone at Enterprise are intermediate between those for the aspen and the maple–birch areas (Table 4). On the basis of the 110 m^2 sampled in each area for diversity, both the midecotone and the maple–birch areas have six canopy species, and the aspen area has five. Differences in diversity reported here are therefore attributable in large part to dissimilarities in the equitability component of diversity rather than to the variety component. Auclair and Goff (1971) reported lower ID values, ranging from 1.04 to 1.73 in forests of the western Great Lakes area, but their values were based on trees of 10 cm or more in dbh.

Seedling diversity exceeds canopy diversity, except in the midecotone. In the aspen area the greater seedling diversity is attributable to a greater number of seedling species and a more even distribution of individuals across species. In the maple–birch area, however, the higher value is due solely to a greater number of species in the seedling stratum because E for seedlings is less than that for canopy trees (Table 4). The ID of seedling species in the midecotone is 1.93, whereas the canopy ID is 2.08, even though the seedling stratum has two more species than the canopy stratum. The reason is related to the comparatively high relative density of *A. balsamea* in the seedling stratum; this results in a low E. Relative to the canopy and seedling strata, sapling diversity is low in the maple–birch area, intermediate in the aspen area, and high in the midecotone.

Table 6

SIMILARITY OF TREE SPECIES COMPOSITION BETWEEN THE THREE AREAS

Areas compared	SC*		
	Seedlings	Saplings	Canopy
Aspen/Midecotone	0.78	0.76	0.54
Midecotone/Maple–birch	0.80	0.76	0.50
Aspen/Maple–birch	0.82	0.70	0.67

*SC (similarity coefficient) = 2c/(a + b), where the two units being compared contain a and b numbers of species, respectively, and have c number of species in common (see Greig-Smith, 1964).

The final measure of forest maturity considered is leaf-area index (LAI). Mature forests with closed canopy and extensive vertical stratification tend toward high values of LAI. The LAI of 4.7 in the midecotone is intermediate to the values of 3.9 in the aspen area and 5.5 in the maple–birch area (Fig. 4). These values include the foliage area of shrubs, the most abundant of which is *Corylus cornuta,* which constitutes more than 50% of all shrubs (Chap. 13, this volume). On the basis of data reported by Tadaki (1966), the average LAI of worldwide, deciduous, broad-leafed forests ranges from approximately 4 to 6. Peterson, Chan, and Cragg (1970) found an average LAI of 4.8 in a *P. tremuloides* grove near Calgary, Alberta, Canada. The values of LAI reported here are therefore within the range of values in the literature.

The main objective of this discussion has been to relate the three principal segments of the ecotone spanning the aspen and maple–birch forest types within a framework of maturity or successional status. All indicators (i.e., canopy composition, understory-canopy similarity coefficients, canopy diversity, and leaf-area index) lead to the conclusion that the three areas studied are all successional in character and exhibit a gradient of increasing maturity from the aspen area to the maple–birch area. The midecotone seems to represent a buffer area between the early successional aspen area and the more mature maple–birch area. The close proximity of the two forests of different maturity is probably a result of different degrees of disturbance, primarily logging, in the area in the recent past. If left completely undisturbed, the aspen area may well succeed toward a northern hardwood climax forest without passing through the disturbance-modified seral stages represented by the adjacent midecotone and maple–birch areas. Some authors would not consider the interface between forest types of different maturity to qualify as a true *ecotone* (Shelford, 1963), but the term is retained here to indicate a zone of transition.

Predicted Effects of Irradiation Along the Ecotone

Zavitkovski and Rudolph (Chap. 13) predicted the overall effects of chronic gamma irradiation on the forest on the basis of reported relations between interphase chromosome volume (ICV) and radiosensitivity. They expect that only scattered herbaceous plants will survive within 15 m of the source and that some shrubs and small radioresistant trees will survive between 15 and 20 m. Presumably tree seedlings could also survive in this zone where the microrelief affords adequate shielding. Of the species found to be important in the ecotone, surviving trees just outside the 20-m radius should include *T. americana* and *P. serotina.* Further back, but within 30 m, some *A. rubrum, A. saccharum, B. papyrifera,*

and *P. tremuloides* should survive. Finally, beyond 30 m of the source, the forest is expected to be essentially unchanged, except that gymnosperms may be eliminated as far back as 50 m.

If the pattern described proves to be approximately correct, the most interesting radial increment for close examination will be between 15 and 30 m from the source; within this zone forest succession will be measurably set back without being totally destroyed. The apparent effects of irradiation will undoubtedly include a severe reduction in both leaf-area index and the number of viable trees along the entire ecotone. The LAI will probably be reduced to near zero out to at least 20 m from the source. The diversity of trees will be reduced all along the ecotone as radiosensitive species are eliminated.

Differences in the severity of the initial effects in the three main areas of the ecotone should be entirely related to floristic differences since there are no major topographical features to alter radiation gradients. The aspen area should experience the greatest aboveground damage because *P. tremuloides* and *A. rubrum*, which have larger ICV values than most of the other ecotone canopy species (Chap. 13, this volume), compose 86.8% of the canopy trees in the aspen area. In the midecotone *P. serotina* and *T. americana* compose 25.9% of the canopy. Since these species have relatively small ICV values, they should be relatively resistant. In addition, *A. saccharum*, which has an intermediate ICV, constitutes 18.5% of the midecotone canopy. Because the maple–birch area is composed largely of *A. rubrum* (37.2%) and *B. papyrifera* (19.6%), both of which have relatively large ICV values, it should show strong radiation effects. However, it also has the most diverse canopy composition of the three areas, and some of the low-density species in the canopy, e.g., *A. saccharum* (11.8%), *P. serotina* (7.8%), and *Ostrya virginiana* (5.9%), are expected to be relatively radioresistant. On the basis of these observations, the aspen area is predicted to display the greatest reduction in number of viable trees and, therefore, the greatest change in overall community structure. The mid-ecotone and maple–birch areas will undergo less structural change, and the degree of mortality in these two areas should be approximately the same since they have similar proportions of radiosensitive species.

McCormick (1970) found that seedling diversity was reduced in proportion to radiation exposure in a tropical rain forest in Puerto Rico. The seedling stratum of the midecotone may be more drastically changed than the seedling strata in the other two areas because *A. balsamea*, a gymnosperm having a large ICV, accounts for 54.6% of all tree seedlings in that area. But the extent of seedling mortality will probably depend partially on the extent of shielding afforded by microrelief. Many of the *A. balsamea* seedlings, for instance, are only a few centimeters in height and are protected behind rocks, stumps, and logs. The consequences of this shielding are impossible to predict.

The nature of recovery along the ecotone during the first and subsequent growing seasons after irradiation will depend on a number of interrelated factors. Root sprouting from *P. tremuloides* with dead aboveground portions can be expected to occur rapidly in the aspen area and the midecotone where the species is abundant. This will probably mean that of the three areas, the aspen area will return most rapidly to its preirradiation condition, which was early successional. Stump sprouting from *A. rubrum*, *A. saccharum*, and other species will also occur along the ecotone.

An important factor influencing the nature and rate of recovery concerns the seedling stratum of each area. The growth rates of those seedlings (especially *A. rubrum*) which, because of low growth form and consequent shielding, survive irradiation will be enhanced by the opened canopy. Existing seedlings could, therefore, contribute significantly to recovery unless they are suppressed by competition from other plants, especially the shrub *C. cornuta*. *Corylus cornuta* is expected to be fairly radioresistant (Chap. 13, this volume) and, because of its great abundance throughout the radiation area, will probably proliferate under the opened canopy. A similar phenomenon was observed in the tropical rain forest study referred to previously (McCormick, 1970). Under the open canopy immediately surrounding the radiation source, one radioresistant shrub species (*Palicourea riparia*) increased its density by a factor of more than 25 the year following irradiation.

As evidenced by the richness of the climax vegetation, environmental conditions are quite favorable during the growing season in northern Wisconsin. The shortness of the season should act as a major constraint on the long-term rate of forest recovery, however. Complex biotic relations, such as competition between tree seedlings and *C. cornuta*, will strongly influence the nature of recovery in the highly disturbed but forested area within 20 to 30 m of the radiation source. The close proximity of undamaged forest to the irradiated area will allow a diverse and probably abundant input of seeds, but it is impossible to predict the germination success and survival that can be expected if understory shrubs and herbs become dense. Immediately after irradiation the structure of the forest ecotone will reflect primarily the elimination of component trees by radiation, but during subsequent growing seasons the structure will reflect changes in biotic and environmental relations.

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Temporal and Spatial Patterns of Pretreatment Litter Production in Site 1 and the Control Area

9

THOMAS R. CROW
Institute of Forest Genetics, North Central Forest Experiment Station, Forest Service, U. S. Department of Agriculture, Rhinelander, Wisconsin

ABSTRACT

Between August 1969 and May 1972, year-round collections of litter fall were obtained in aspen, birch, and northern hardwood communities in site 1 and similar communities in the control area of the Enterprise Radiation Forest. In both areas total litter production was greatest in the northern hardwood forest type, intermediate in birch, and lowest in aspen. The differences proved statistically significant in the control area but not in site 1 ($P > 0.05$). Differences among years were also significant in terms of total litter production but were not significant for leaf-litter production. Because of its spatial and temporal (on an annual basis) uniformity relative to other litter components, leaf litter should provide the best indicator of perturbation related to chronic gamma irradiation. The estimated mean annual production (all types) was 316 g dry weight per square meter for total litter: 234 g/m^2 for leaf litter (74% of the total), 50 g/m^2 for twigs (16% of the total), 27 g/m^2 for the miscellaneous component (8% of the total), and 5 g/m^2 for seeds (2% of the total).

The ease with which litter fall can be measured and the myriad of possible relationships that can be pursued with litter-fall information make it a valuable parameter in an ecosystem study. For example, the importance of litter production in the transfer of nutrients and energy within a vegetative community is intuitive. Relationships could be investigated between litter production and environmental factors (e.g., throughfall of rain and insolation reaching the forest floor), community attributes (e.g., standing crop, net primary production, stocking density, species diversity), and even such physiological processes as photosynthesis and respiration. Of primary importance in a study of the impact of chronic gamma irradiation on a vegetative community is the use of litter-fall information as an indicator of disturbance. Such an application, as demonstrated by Woodwell and Marples (1968), can be made more effectively when we have sufficient knowledge of the intrinsic variation in the natural state. This paper summarizes three years of pretreatment litter-collection data from the Enterprise Radiation Forest site 1 and the control area, with emphasis on temporal and spatial patterns of variation.

METHODS

Beginning in August 1969, litter-fall collections were made in three forest types in a site selected for exposure to radiation during the growing season (site 1) and in corresponding types in a control area. The forest types, initially designated as aspen, birch, and northern hardwood, are floristically less distinctive than the type names imply. A complete discussion and description of these forest types is presented by Zavitkovski (Chap. 6, this volume).

In view of the desire to study changes in litter production along proposed gradients of irradiation, traps in site 1 were placed along transects originating at the proposed location of the radiation source and extending at a randomly chosen azimuth to a point 150 m from the source. Twelve traps (0.5 by 0.5 m square) were located in each of the three forest types at 10, 20, 40, 70, 110, and 150 m from the source; each location had two traps. In the corresponding forest types of the control area, the location of the initial trap was randomized and four subsequent traps were located at points 20 m apart along a transect within each type.

The traps were a combination litter and seed trap in which the large materials, such as leaves and twigs, were collected in the upper tray and finer materials, such as seeds and insect frass, filtered through the coarse 6-mm mesh of the upper tray into the more protected confines of the lower tray (1-mm window screen). Litter traps are obviously inadequate for sampling the larger fractions of litter, such as branch or bole material. Collection of these materials from ground plots was initiated in 1972 but is not reported here. Therefore "total litter" refers to only the tree and shrub litter collected in the litter traps.

Traps were emptied monthly, except in September and October when heavy leaf fall necessitated collection twice a month. Material was sorted into leaf, twig, seed, and miscellaneous components and oven-dried at 70°C. A collection year is defined as extending from May, the approximate initiation of the growing season, through the following April.

Unless otherwise stated, statistical tests of significance are expressed at the 0.05 probability level.

RESULTS AND DISCUSSION

Annual Production of Litter

In terms of total litter, mean annual production for all stands ranged from a low of 256 g dry weight per square meter in 1969-1970 to 332 g/m^2 in 1971-1972. The low figure, however, represents less than a full year of collection (August 1969 to April 1970). When based on the

two full years of collection (1970-1971 and 1971-1972), the estimated mean annual production is 316 g/m^2 for total litter: 234 g/m^2 for leaf litter, 50 g/m^2 for twigs, 27 g/m^2 for the miscellaneous component, and 5 g/m^2 for seeds. When a correction factor, derived from 1970-1972 data for the portion of litter fall prior to August, is applied to the 1969-1970 data, the estimate is increased from 225 to 235 g/m^2 for leaf litter and 256 to 294 g/m^2 for total litter. The total range is then 232 to 235 g/m^2 for leaf litter and 294 to 332 g/m^2 for total litter (Table 1). These estimates are somewhat below the figures of 250 and 350 g/m^2 often cited for leaf and total litter fall, respectively, in cool temperate forests (Bray and Gorham, 1964), but are within the ranges of 200 to 300 g/m^2 for leaf fall (Tadaki, 1966) and 300 to 400 g/m^2 for total litter fall (Rodin and Bazilevich, 1967) which seem inclusive of deciduous forests regardless of region.

Table 1

WEIGHTED MEAN ANNUAL PRODUCTION FOR ALL COLLECTION AREAS AT ENTERPRISE FOREST

Collection year	Litter production, dry weight, g/m^2
Leaf Litter	
1969-1970	225*
1970-1971	232
1971-1972	235
Total Litter	
1969-1970	256†
1970-1971	300
1971-1972	332

*Corrected to full year: 235 g/m^2.
†Corrected to full year: 294 g/m^2.

Table 2

LITTER-PRODUCTION SUMMARY, AUGUST 1969 TO APRIL 1970

Forest type	Values*	Seed	Leaves	Twigs	Other	Total
Site 1						
Aspen	Mean, dry weight,† g/m^2	1.79	198.80	36.70	7.82	245.13
	SD	2.32	60.07	53.42	2.46	76.49
	SE	0.67	17.34	15.42	0.71	22.08
	CV, %	129.6	30.2	145.6	31.5	31.2
Birch	Mean, dry weight,† g/m^2	2.85	216.80	25.50	13.12	258.27
	SD	3.85	74.62	46.12	6.36	102.58
	SE	1.12	21.54	13.31	1.84	29.61
	CV, %	135.1	34.4	180.9	48.5	39.7
Northern hardwood	Mean, dry weight,† g/m^2	2.67	226.26	6.60	10.84	246.38
	SD	1.42	130.08	7.70	4.43	105.04
	SE	0.41	29.76	2.22	1.28	30.32
	CV, %	53.2	57.5	116.7	40.8	42.6
Control Area						
Aspen	Mean, dry weight,† g/m^2	0.62	182.44	14.18	5.56	202.81
	SD	0.38	17.61	13.66	2.66	16.56
	SE	0.17	7.87	6.11	1.19	7.41
	CV, %	61.3	9.6	96.3	47.8	8.2
Birch	Mean, dry weight,† g/m^2	0.81	272.77	3.92	6.98	284.47
	SD	0.56	31.84	2.20	1.36	30.71
	SE	0.25	14.24	0.98	0.61	13.74
	CV, %	69.1	11.7	56.1	19.5	10.8
Northern hardwood	Mean, dry weight,† g/m^2	0.56	305.14	8.67	10.74	325.10
	SD	0.27	20.85	10.32	4.26	25.57
	SE	0.12	9.32	4.61	1.90	11.43
	CV, %	48.2	6.8	119.0	39.7	7.9

*Abbreviations are: SD, standard deviation; SE, standard error of the mean; CV, coefficient of variation.
†g/m^2 x 10= kg/ha; kg/ha x 0.89 = lb/acre.

The mean, standard deviation (SD), standard error of the mean (SE), and coefficient of variation (CV) for the production of each litter component by forest type and collection year are presented in Tables 2 to 4. Other estimates of litter production at Enterprise do exist and are of comparative interest. Immediately following the completion of leaf fall in 1971, Murphy, Sharitz, and Murphy (Chap. 10) collected leaves from ground plots in the aspen and northern hardwood (maple–birch) areas in site 1. Their estimated production of tree and shrub leaf litter was 2.32 tonnes/ha for aspen and 2.63 tonnes/ha for maple–birch. These estimates are similar to those based on trap catches—2.34 tonnes/ha for aspen and 2.71 tonnes/ha for northern hardwood (Table 4). The figures seem to indicate that the wind caused no great losses of leaves from traps. A second comparison indicates the ability of the traps to retain the smaller litter components. In early spring 1971 traps designed to catch and retain the light windblown seeds of aspen (*Populus tremuloides* Michx. and *Populus grandidentata* Michx.) were placed at the same locations as the litter traps. These circular seed traps, equal in cross-sectional area to the standard litter traps, were constructed by stapling 1-mm window screen to lath sticks. A double layer of cheesecloth was then stretched across the bottom of the trays and attached to the screen with pins. Because of the depth of these traps, it is unlikely that litter was blown out, and repeated washings indicated that there were no measurable losses through the cloth during rain. Based on a t-test, differences between these two types of traps in the collection of nonwoody litter were not significant in any of the three treatment or control forest types. During May 1971, the period of comparison, the production of small miscellaneous litter (mainly bud scales and inflorescences) was 3.44 g/m^2 based on the standard litter traps and 3.80 g/m^2 based on the circular seed traps.

Relative Portions of Components

During the full years of collection, nonleaf litter averaged 26% of total litter fall, a figure comparable to the estimate of 21% by Bray and Gorham (1964) for cool, temperate forests. Nonleaf litter accounted for only 12% of total fall collected in 1969-1970, the less than

Table 3

LITTER-PRODUCTION SUMMARY, MAY 1970 TO APRIL 1971

Forest type	Values*	Seed	Leaves	Twigs	Other	Total
		Site 1				
Aspen	Mean, dry weight,† g/m²	3.72	222.71	45.83	17.51	289.76
	SD	2.97	64.76	42.16	4.81	75.88
	SE	0.86	18.69	12.17	1.21	21.90
	CV, %	79.8	29.1	92.0	23.9	26.2
Birch	Mean, dry weight,† g/m²	6.49	191.85	61.71	20.06	286.27
	SD	7.56	43.67	83.83	9.27	107.15
	SE	2.18	12.61	24.20	2.68	30.93
	CV, %	116.5	22.8	135.8	35.6	37.4
Northern hardwood	Mean, dry weight,† g/m²	3.08	292.82	30.73	28.05	354.68
	SD	2.22	88.19	20.96	7.11	90.79
	SE	0.64	25.46	6.05	2.05	26.21
	CV, %	72.1	30.1	68.2	25.3	25.6
		Control Area				
Aspen	Mean, dry weight,† g/m²	1.46	167.18	58.27	13.01	239.92
	SD	1.15	10.82	48.77	3.34	56.78
	SE	0.51	4.84	21.81	1.49	25.39
	CV, %	78.8	6.5	83.7	25.7	23.7
Birch	Mean, dry weight,† g/m²	0.95	215.94	23.86	20.14	260.90
	SD	0.62	30.05	12.26	2.34	33.64
	SE	0.28	13.44	5.48	1.04	15.04
	CV, %	65.3	13.9	51.4	11.6	12.9
Northern hardwood	Mean, dry weight,† g/m²	0.76	285.46	18.30	24.18	328.69
	SD	0.85	58.02	30.30	4.03	64.01
	SE	0.38	25.93	13.55	1.80	28.63
	CV, %	111.8	20.3	165.6	16.7	44.7

*Abbreviations are: SD, standard deviation; SE, standard error of the mean; CV, coefficient of variation.

†g/m² x 10 = kg/ha; kg/ha x 0.89 = lb/acre.

full-year collection; this difference can be attributed largely to the lack of spring litter and to the smaller collections of twigs (Table 5). The importance of fruits and floral structures to total litter has been emphasized by Ovington (1963); however, the magnitude of these components which he reported for birch and aspen stands did not show up in our study. In a birch stand at Holme Fen, the weight of birch seed equalled 8.2% of the leaf weight (Ovington, 1963); during the most productive seed year at Enterprise, birch seed equalled 3% of the leaf weight. The largest contribution by seeds at Enterprise was in northern hardwoods. During a year of abundant red maple (*Acer rubrum* L.) seed production, seeds alone represented 3.5% of total litter fall and 4.6% of leaf fall in the site 1 northern hardwood area. Catkins were not weighed separately in this study, but the entire miscellaneous category, of which catkins were a component, never reached the 25.8% of leaf weight which was reported by Ovington for aspen catkins in a Minnesota stand. An additional factor of importance in the spring, bud scales, accounts for a large portion of the miscellaneous category in this study. In summary, the proportions represented in the last two collection years in Table 5 are more indicative of the norm, with the last year representing a period of abundant production of inflorescence and seed.

Spatial and Temporal Variation

The range, mean value ($\bar{x}$), and 95% confidence limits for the population mean (μ) are presented by forest type and year for total litter (Fig. 1) and for leaf litter (Fig. 2). In both the control area and site 1, total litter production appears to be greatest in the northern hardwood forest type, intermediate in birch, and lowest in aspen. Based on analysis of variance (Table 6), differences among forest types did prove significant ($P < 0.05$) in the control area but not in site 1. This fact is not surprising since there is greater homogeneity within types and greater heterogeneity among types in the control area than in site 1. However, the obvious differences between the control area and site 1 in variation (see Fig. 1), as measured by the total range of annual catches, can be attributed only partially to the rather striking differences in the homogeneity of vegetation. The smaller sample size is also a factor, and thus the coefficients of variation in Tables 2 to 4 are more indicative of the inherent variability.

Two additional components of variation, among traps and among years, proved to be important in the analysis of variance for total litter. In both the control area and site 1, differences among traps and differences among years were significant.

Unlike total litter, leaf-litter production was not significantly different among years in site 1 and the control area (Table 6). Total litter and leaf-litter production were similar in that differences among traps were significant in both areas and differences among forest types were significant only in the control area.

Some of the differences among traps are no doubt related to dissimilarities within cover types. According to Zavitkovski (Chap. 6) changes in cover occur at the 50-m radius in both the northern hardwood and birch communities of site 1. The northern hardwood community, according to Zavitkovski, should be designated a maple–aspen–birch forest type within 50 m of the source and a more typical northern hardwood type dominated by sugar maple (*Acer saccharum* Marsh.) and basswood (*Tilia americana* L.) between 50 and 150 m from the source. In addition, the birch stand within 50 m is located on a wet plateau, whereas the stand between 50 and 150 m is a dry–mesic forest. These dissimilarities are reflected in differences in litter production in northern hardwoods but not in birch (Table 7). Litter production in the 50- to 150-m sector of hardwoods exceeded that in the 50-m sector during all three years, and the difference was statistically significant in two of the three years. No significant

differences were found for comparisons within birch communities.

With the exception of control birch, consecutive yearly increases in total litter production are shown for all types in Fig. 1. Since annual variation in leaf fall does not follow this monotonic trend (Fig. 2), the consistent increases are from nonleaf components of litter. The previously mentioned lack of spring collections during 1969 is one factor in this observed trend. An additional factor is the increased frequency of woody litter in the traps in consecutive sampling periods.

To test for consistency in spatial and temporal patterns of variation along transects, we ranked trap collections from low to high for each collection year and applied a Spearman rank correlation (Table 8). The nonparametric test was used to avoid difficulties due to differences between total collections during the partial-year collection of 1969-1970 and subsequent full-year collections. The parameter of concern was relative rank, not comparison of absolute weights. Because of restricted degrees of freedom, rank correlations were not applied to collections in the control area.

In the site 1 data, significant correlations were frequent only for the leaf component of litter. Based on the uniformity of leaf-litter production at Enterprise and on past work at Brookhaven (Woodwell and Marples, 1968), leaf collection should provide a sensitive indicator of radiation damage. The consistencies in patterns of leaf fall are not reflected in the patterns of total litter fall, and thus it appears that leaf fall will be of greater utility as a gauge of radiation stress. In addition, no significant correlations were found for twigs or for the miscellaneous component, and only two significant correlations were found for seeds. The lack of significant correlations for twig litter can be attributed partially to an inherent characteristic, its sporadic occurrence in time and space, and partially to a sampling design that is inadequate to sample this diversity. Despite its lack of uniformity as measured by litter traps, woody litter should also be useful as an indicator of disturbance. Additional collections (ground plots in addition to traps) are being made of this component because an increased flux is expected to follow mortality caused by irradiation. Miscellaneous litter and seeds are also variable components. It should be noted, however, that during a year of abundant seed production, the third collection year, the spatial variability of this component as measured by the coefficient of variation in Table 4 was at a minimum and in one case, site 1 northern hardwood, the spatial uniformity of seed fall compared to that of leaf fall. The abundant production of propagules following irradiation is a definite possibility, and thus a potential correlation exists between seed production and radiation damage. Relationships between total seed production, proportions of viable seed, and accumulated dosage will be investigated in the posttreatment evaluation.

Figure 3 expresses the pretreatment collection of leaf litter along the transects. From this figure we get an idea of the pattern of changes along each transect, the consistency of this pattern from year to year, and the magnitude of the differences from station to station and year to year. The trends reflect largely the previously discussed degree of homogeneity within each stand. The most homogeneous stand, aspen, has the most uniform trend. The 10-m traps in aspen border a road that runs through the area and thus are biased downward. Annual collections at 40, 70, 110, and 150 m show exceptional precision during the three years of collection, and posttreatment declines in foliage production as small as 10 to 15% should be detectable. It is questionable whether change at this scale in the birch and northern hardwood stands will be detectable. The smallest yearly variation in birch was 40 g/m^2 at the 40-m collection station, and at one station (at 70 m) the average leaf collections varied by a factor greater than 2. Annual variations in northern hardwoods were often 100 g/m^2, and there was an abrupt upward change in trend, which is

Table 4

LITTER PRODUCTION SUMMARY, MAY 1971 TO APRIL 1972

Forest type	Values*	Seed	Leaves	Twigs	Other	Total
		Site 1				
Aspen	Mean, dry weight,† g/m^2	7.63	233.83	59.48	26.18	327.12
	SD	5.68	68.26	39.48	7.46	72.93
	SE	1.64	19.70	11.54	2.15	21.05
	CV, %	74.4	29.2	66.4	28.5	22.3
Birch	Mean, dry weight,† g/m^2	7.15	214.85	75.17	35.55	332.73
	SD	3.34	73.94	64.13	14.91	120.70
	SE	0.96	21.34	18.51	4.30	34.84
	CV, %	45.7	34.4	85.3	41.9	36.3
Northern hardwood	Mean, dry weight,† g/m^2	12.47	270.72	33.11	44.14	360.45
	SD	2.73	62.13	26.29	19.86	82.96
	SE	0.79	17.94	7.59	5.73	23.95
	CV, %	21.9	22.9	79.4	45.0	23.0
		Control Area				
Aspen	Mean, dry weight,† g/m^2	2.91	170.84	60.67	20.72	255.38
	SD	1.83	33.42	63.67	2.80	70.80
	SE	0.82	14.95	28.47	1.25	31.66
	CV, %	62.9	19.6	104.9	13.5	27.7
Birch	Mean, dry weight,† g/m^2	6.83	214.62	36.90	31.94	290.27
	SD	4.83	28.21	24.65	4.82	44.78
	SE	2.16	12.62	11.03	2.15	20.02
	CV, %	70.7	13.1	66.8	15.1	15.4
Northern hardwood	Mean, dry weight,† g/m^2	4.26	287.78	67.90	31.25	391.18
	SD	2.38	39.19	60.48	2.65	70.01
	SE	1.07	17.53	27.05	1.19	31.31
	CV, %	55.9	13.6	89.1	8.5	17.9

*Abbreviations are: SD, standard deviation; SE, standard error of the mean; CV, coefficient of variation.

†g/cm^2 x 10 = kg/ha; kg/ha x 0.89 = lb/acre.

Table 5

RELATIVE CONTRIBUTIONS OF LITTER COMPONENTS TO TOTAL LITTER BY COLLECTION YEAR AND AREA

Area*	Mean percent of total litter				Number of traps
	Seed	Leaves	Twigs	Other	
		1969-1970†			
A1	0.7	81.1	15.0	3.2	12
B1	1.1	83.9	9.9	5.1	12
NH1	1.1	91.8	2.7	4.4	12
CA	0.3	89.9	7.0	2.7	5
CB	0.3	95.9	1.4	2.4	5
CNH	0.2	93.9	2.7	3.3	5
Weighted mean	0.76	87.84	7.58	3.82	
		1970-1971‡			
A1	1.3	76.9	15.8	6.0	12
B1	2.3	67.0	21.5	7.0	12
NH1	0.9	82.6	8.7	7.9	12
CA	0.6	69.7	24.3	5.4	5
CB	0.4	82.8	9.1	7.7	5
CNH	0.2	86.8	5.5	7.3	5
Weighted mean	1.18	77.26	14.64	6.92	
		1971-1972‡			
A1	2.3	71.5	18.2	8.0	12
B1	2.1	64.6	22.6	10.7	12
NH1	3.5	75.1	9.2	12.2	12
CA	1.1	66.9	23.8	8.1	5
CB	2.3	73.9	12.7	11.0	5
CNH	1.1	73.6	17.3	8.0	5
Weighted mean	2.30	70.73	17.04	9.93	

*Abbreviations are: A1, site 1 aspen; B1, site 1 birch; NH1, site 1 northern hardwood; CA, control aspen; CB, control birch; CNH, control northern hardwood.

†Less than full collection year (August to April).

‡Full collection year (May to April).

probably a product of the change in cover type at this point (between the 40- and 70-m collection points).

The strong seasonality of total litter fall is obvious in Figs. 4 to 7, in which monthly litter fall is expressed as a percentage of annual fall for forest types in site 1 and the control area. Considering both years shown and all collection areas, litter fall during September and October, represented almost entirely by leaf biomass, averaged 77% of total annual fall and ranged from 61 to 85%. A steady flux of litter fall was recorded during spring and summer, with some anomalies due to large collections of woody litter (e.g., the June 1970 collection in the control aspen stand, Fig. 4). Collections from December to March yielded extremely small amounts of litter, in no case exceeding 1% of the total annual collection; therefore periodic collections during winter at Enterprise are difficult to justify unless one is attempting to relate litter fall to the occurrence of high winds or ice storms. In addition, increased fluxes of litter in April indicate that the collection year could logically begin in this month.

In terms of annual leaf fall, 10.2% occurred before the middle of September 1970 (before day 255), but only 4.1% occurred for the same period in 1971. This difference in seasonality of leaf fall between collection years can be seen in Figs. 4 to 7. In all forest types 1970 collections in August and September ex-

Table 6

ANALYSIS OF VARIANCE FOR LEAF AND TOTAL LITTER PRODUCTION

Component of variation	Litter component		Degrees of freedom
	Total	Leaf	
	Site 1		
Collection year	*	NS†	2
Cover type	NS	NS	2
Trap	*	*	11
	Control Area		
Collection year	*	NS	2
Cover type	*	*	2
Trap	*	*	4

*$P < 0.05$.

†Abbreviation NS = not significant.

Table 7

COMPARISON OF TOTAL LITTER PRODUCTION WITHIN AND BEYOND 50 M FROM THE RADIATION SOURCE

Forest type and sector	Mean annual production, dry weight, g/m^2		
	1969-1970	1970-1971	1971-1972
Birch			
<50 m	257.2	342.1	335.3
>50 m	259.3	230.4	330.2
	$t = 0.033$ (NS*) d.f. = 10	= 2.053 (NS) = 5($\sigma_1 \neq \sigma_2$)†	= 0.070 (NS) 10
Northern hardwood			
<50 m	169.7	333.8	313.2
>50 m	323.0	373.2	408.0
	$t = 3.726$ ($P < 0.01$) d.f. = 10	= 0.743 (NS) = 10	= 2.350 ($P < 0.05$) = 10

*Abbreviation NS = not significant.

†Test of equality of means when variances are unequal, degrees of freedom (d.f.) = n − 1.

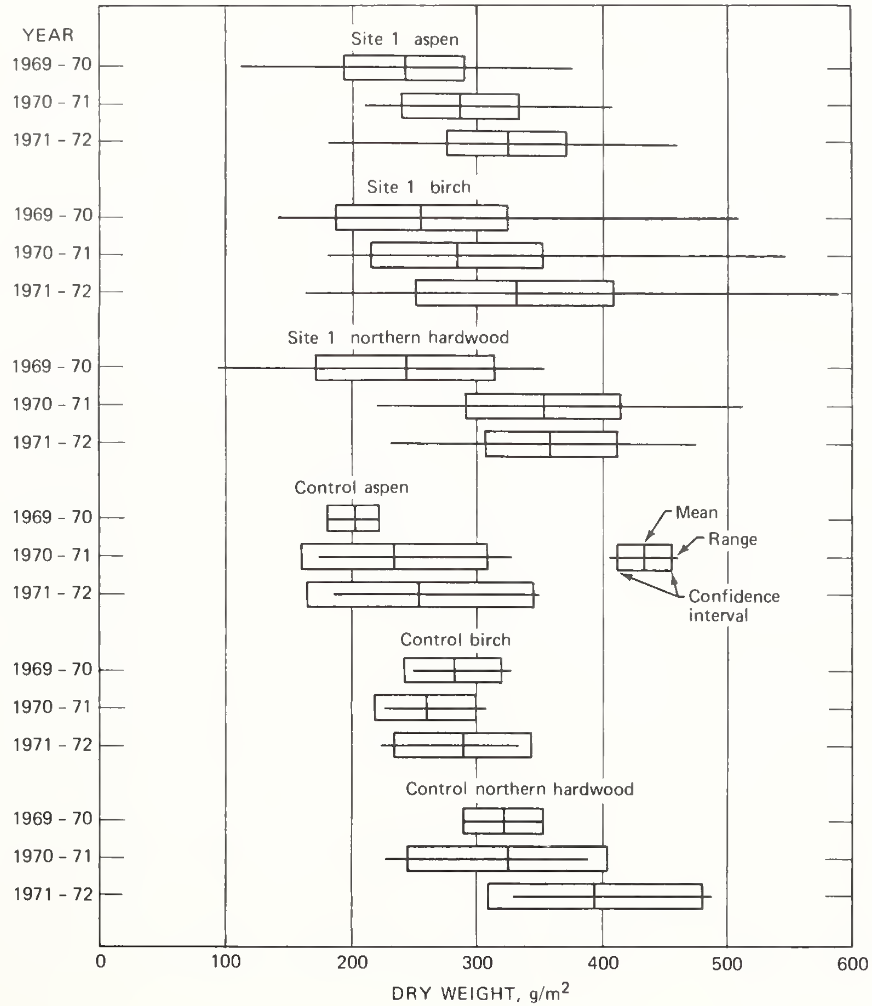

Fig. 1 Mean total litter fall, total range, and 95% confidence interval for population mean by area and collection year.

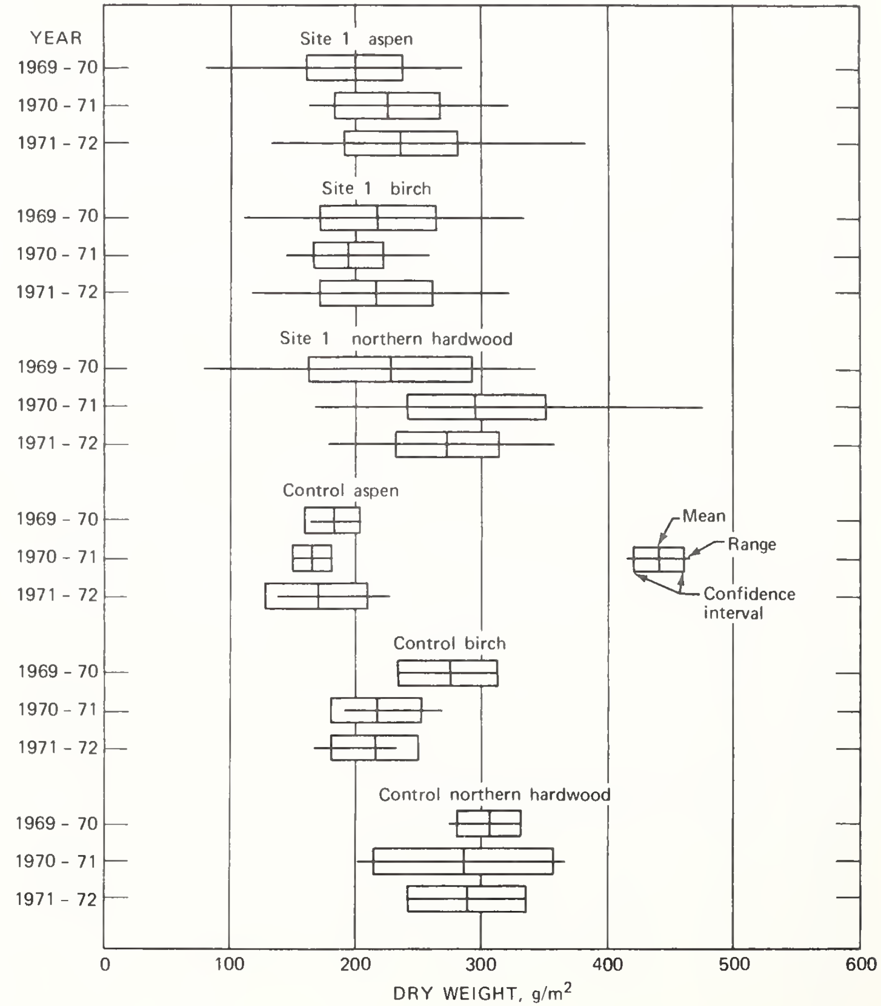

Fig. 2 Mean leaf fall, total range, and 95% confidence interval for population mean by area and collection year.

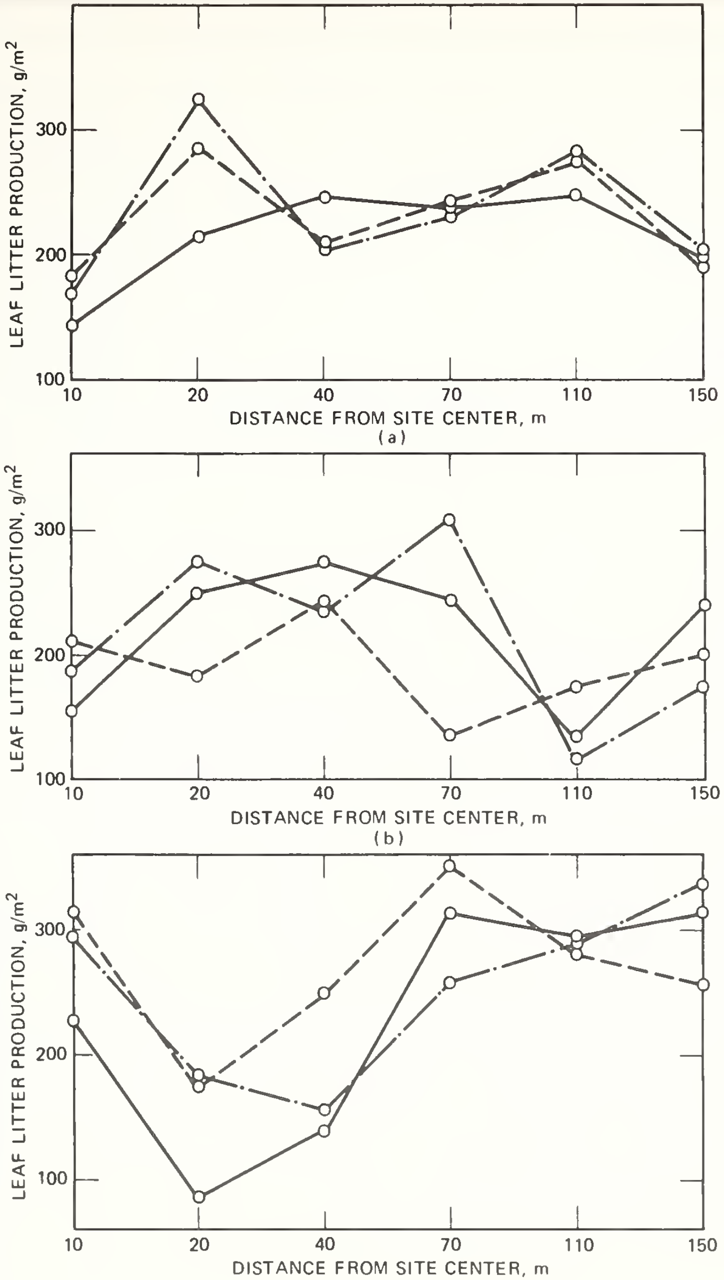

Fig. 3 Leaf collections in site 1. ———, 1969-1970; - - - -, 1970-1971; —·—·, 1971-1972. Each data point represents an average of the two traps at that sampling location. (a) Aspen. (b) Birch. (c) Northern hardwood.

Table 8

SPEARMAN RANK CORRELATION OF INDIVIDUAL TRAP COLLECTIONS WITHIN FOREST TYPES BETWEEN YEARS OF PRETREATMENT LITTER COLLECTION (12 TRAPS)

Forest type	Litter component	Comparison of collection years* 1 to 2	1 to 3	2 to 3
Aspen	Total	NS†	NS	NS
	Leaf	$P < 0.05$	$P < 0.05$	$P < 0.01$
	Seed	NS	$P < 0.05$	NS
Birch	Total	NS	NS	NS
	Leaf	NS	$P < 0.05$	NS
	Seed	NS	NS	NS
Northern hardwood	Total	NS	$P < 0.05$	NS
	Leaf	NS	$P < 0.01$	NS
	Seed	NS	$P < 0.05$	NS

*Collection year 1, 1969-1970; collection year 2, 1970-1971; collection year 3, 1971-1972.

†Abbreviation NS = not significant.

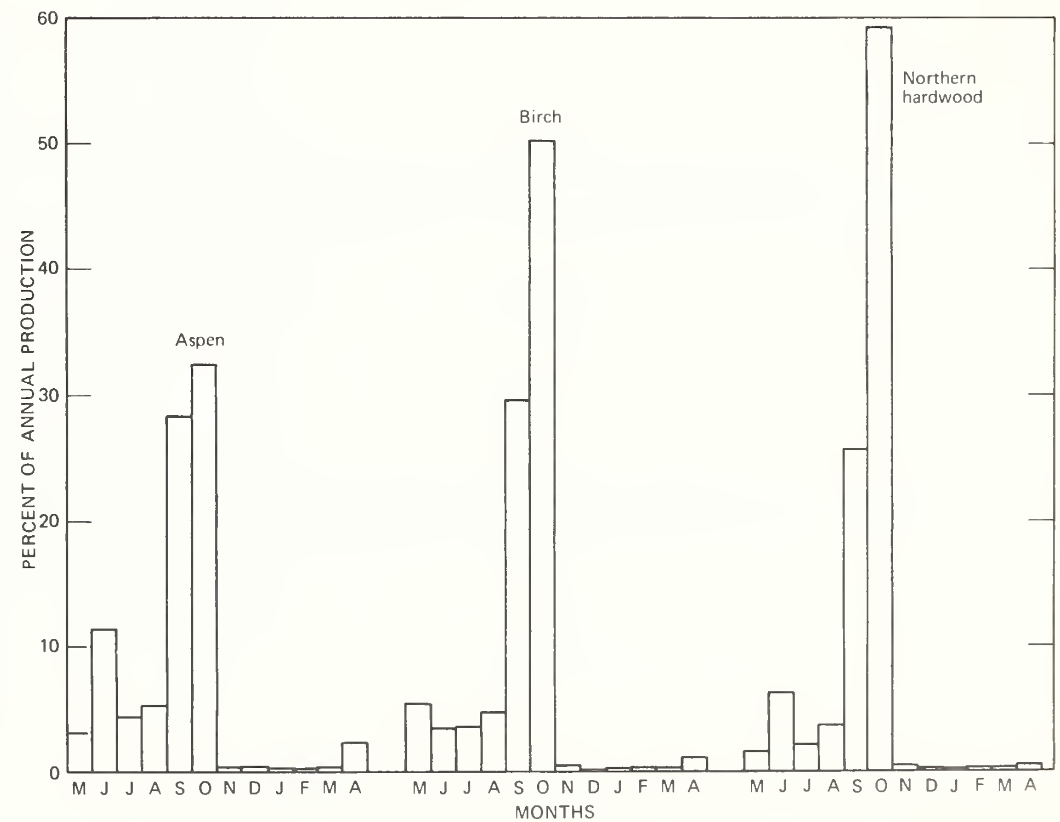

Fig. 4 Relative distribution of total litter fall during the 1970-1971 collection year (May to April) in the control area.

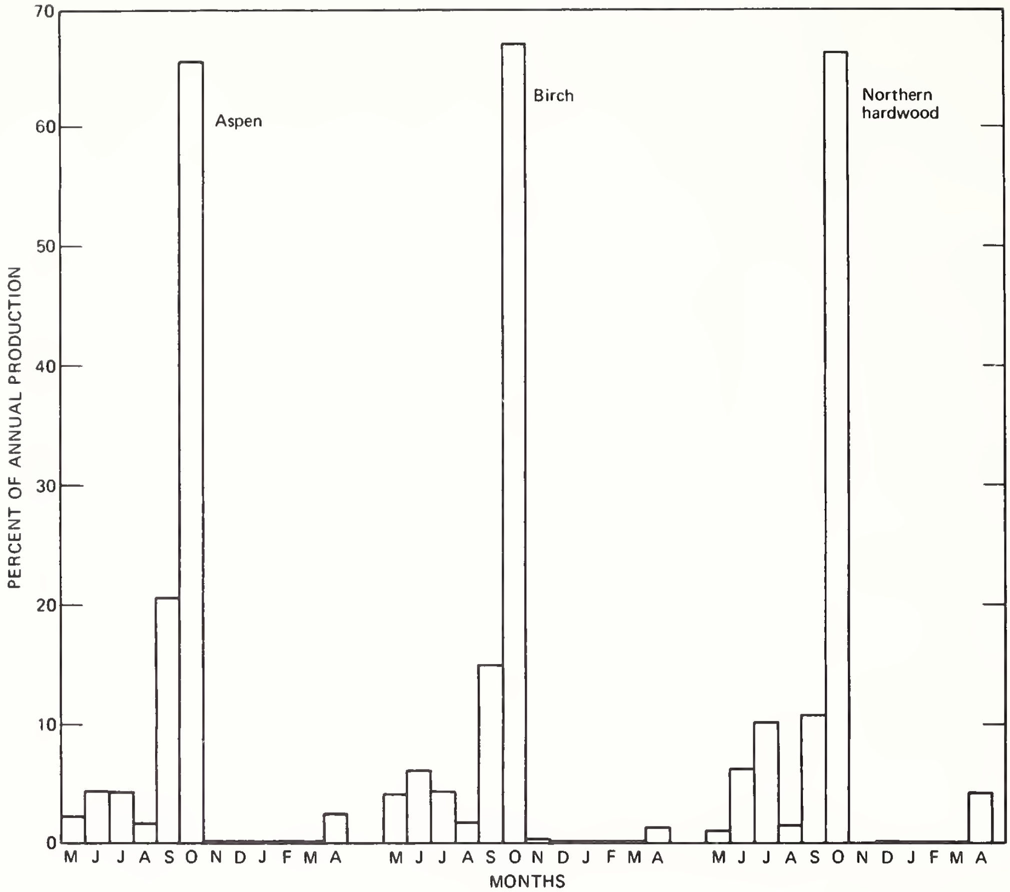

Fig. 5 Relative distribution of total litter fall during the 1971-1972 collection year (May to April) in the control area.

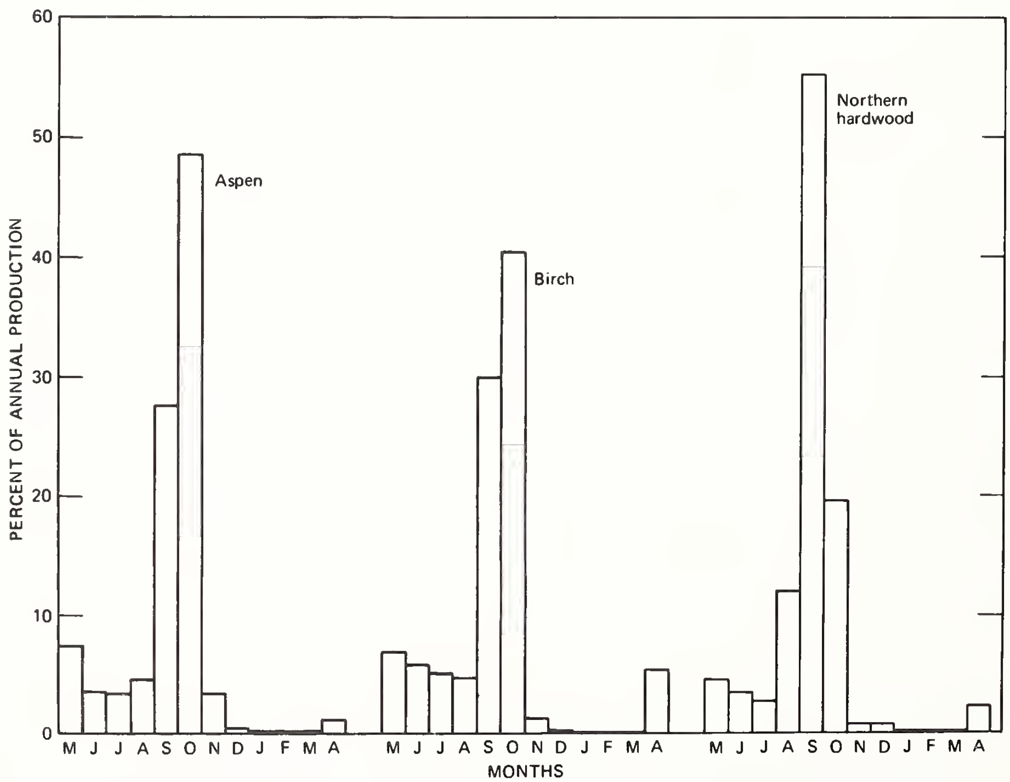

Fig. 6 Relative distribution of total litter fall during the 1970-1971 collection year (May to April) in site 1.

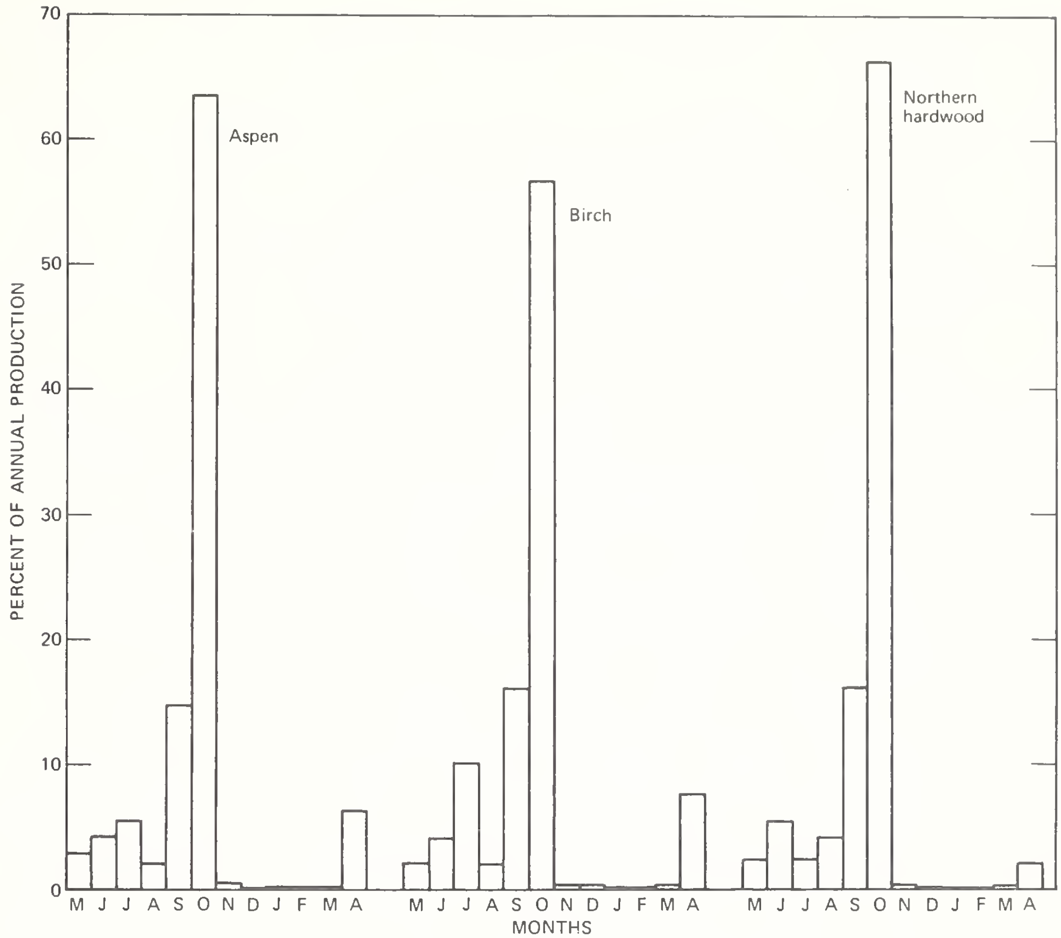

Fig. 7 Relative distribution of total litter fall during the 1971-1972 collection year (May to April) in site 1.

ceeded those in the same months for the following year; an inverse pattern exists for October and November. On the basis of climatic conditions (a drought occurred in late summer 1970) and on comparisons with three years of phenological data (Richard Buech, personal communication) and with the absolute weights of the 1969-1970 catches, it is apparent that the 1971-1972 data represent a more typical litter-fall distribution pattern for September and October. It is possible that the initial exposure, a growing-season exposure, will produce changes in seasonal patterns in site 1 similar to those produced by moisture stress in 1970. On the basis of studies in Piedmont hardwoods in Georgia, McGinnis (1963) asserted that lethal or near lethal doses of radiation were necessary to produce pronounced changes in the temporal patterns of leaf shedding. Such dosages will occur only within short distances from the source during a growing-season exposure.

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Leaf-Litter Production in the Aspen and Maple-Birch Forest Types and the Contribution by Individual Tree Species

10

*PETER G. MURPHY,**
REBECCA R. SHARITZ,†
*ALICE J. MURPHY**
*Michigan State University, East Lansing, Michigan
†Savannah River Ecology Laboratory, Aiken, South Carolina

ABSTRACT

Immediately following leaf fall in 1971, leaf-litter samples were collected from two forest types, aspen and maple–birch, and from an intervening zone of transition. Only leaves that fell in 1971 were collected. Leaf-litter fall for trees averaged 134 kg/m^2 of basal area in the aspen area and 142 kg/m^2 in the maple–birch area. Total tree and shrub leaf-litter fall was estimated to be 2.32 tonnes/ha in the aspen area and 2.63 tonnes/ha in the maple–birch area. Shrub leaf-litter fall was greatest in the aspen area, 5.4% of total leaf-litter fall. The relation between relative basal area and relative leaf-litter biomass for tree species was approximately 1 : 1. Diversity values computed on the basis of number of leaves per species or on biomass of leaves per species indicated that the maple–birch foliage was most diverse and the aspen foliage least diverse. This result parallels that found when diversity was based on number of trees per species.

Traditional descriptions of forest composition are based on listings of the plant species, along with various parameters describing the species arrays. Measures of density, frequency, and basal area, or some combination of these parameters, are used most often. Although these measures convey a considerable amount of information, no single index is entirely adequate for a complete description. This is especially true when an analysis of forest structure is intended to offer insight into the characteristics of forest function, such as energy or mineral flow. The elucidation of structure–function relationships requires the close scrutiny and measurement of many types of ecosystem components in a variety of different ways.

The leaves produced by forest trees have long been of interest in regard to their functional roles in the ecosystem. Their important roles in energy flow and mineral cycling are not discussed here. In most studies of forest structure, however, the leaves either are ignored or are described solely in terms of measures that pool the leaves of different species. Such measures include leaf-area index and total leaf biomass per unit area of forest. Among the numerous papers that give special attention to forest foliage are excellent review papers by Bray and Gorham (1964) and Tadaki (1966). Both these papers contain well-documented information concerning leaf biomass production in different types of forests, but both discuss leaf production of the forest stand as a whole rather than of the species within the stand.

The primary objective of this study is to describe several forest types using measures based on leaf composition and to relate this description to one based on whole trees. Three areas of the Enterprise Forest site 1, within 50 m of the radiation source, including two distinctly different forest types and an intervening zone of transition, were investigated.

METHODS

Two of the forest areas studied are named for their dominant canopy species, the aspen area and the maple–birch area. The third area, a transitional zone situated between the other two, is termed the midecotone. Murphy and Sharitz (Chap. 8, this volume) give more-detailed descriptions of the floristic characteristics of these three areas, and Zavitkovski (Chap. 6, this volume) discusses two of the areas, aspen and maple–birch (which he refers to as northern hardwood), on the basis of total tree inventories.

All information concerning forest foliage was obtained from the collection of leaf litter. On Oct. 30, 1971, within one week after leaf fall was complete, leaf-litter samples were collected from the aspen, midecotone, and maple–birch areas. At the time of collection all deciduous trees in the areas sampled, including red oak, were bare of leaves. A portable frame 0.25 m^2 in area was placed on the litter layer, and tree and shrub leaves produced during the 1971 growing season were collected from within the frame. Four such samples were taken at 10, 20, 30, 40, and 50 m from the radiation source in each forest area. Thus 20 samples totaling 5 m^2 in area were collected from each forest area. All leaf-litter samples were air dried, and 10 were also oven dried to determine a factor for conversion from air-dry to oven-dry weight. The air-dried samples lost an average of 8.91% (standard error, 0.19%) of their weight when oven dried for 24 hr at 100°C. This factor (8.91%) was used in all conversions.

On the basis of the oven-dry weight of the 20 samples from each area, the total annual leaf-litter production in metric tonnes per hectare was estimated for each area. In addition, all leaves in each sample were sorted by species, counted, and weighed. More than 30,000 leaves were sorted to obtain estimates of annual leaf-litter production per species and of species diversity.

Several possible experimental errors that may have influenced the data should be mentioned. We had to assume that, for each leaf lost from a sample site, another leaf was introduced from an adjoining

Table 1

ANNUAL LEAF-LITTER PRODUCTION IN THREE FOREST AREAS (1971)

Area	Leaf litter,* tonnes/ha/year		Tree leaf litter, % of total
	Trees + shrubs	Trees only	
Aspen	2.32	2.19	94.6
Midecotone	1.79	1.72	96.1
Maple–birch	2.63	2.56	97.3

*Oven-dry weight.

Table 2

RELATIVE BASAL AREA (RBA)* AND RELATIVE LEAF-LITTER BIOMASS (RLB) FOR TREE SPECIES IN TWO FOREST TYPES

Species	Aspen		Maple–birch	
	RBA, %	RLB, %	RBA, %	RLB, %
Acer rubrum	13.67	13.54	26.34	19.23
A. saccharum	2.95	2.64	11.46	20.95
Amelanchier sp.	0.93	1.57	0.70	0.16
Betula papyrifera	11.18	8.22	17.85	20.62
Carpinus caroliniana				0.03
Fraxinus sp.	1.16	0.05	9.14	0.05
Ostrya virginiana	0.64	3.18	2.16	3.11
Populus grandidentata	0.81	1.42	0.49	0.20
P. tremuloides	54.92	49.79	11.74	11.05
Prunus serotina	5.62	2.00	5.90	3.25
Quercus rubra	7.07	17.12	3.35	17.61
Salix sp.	0.52	0.43	0.11	0.01
Tilia americana	0.06	0.03	6.60	3.69
Ulmus americana			2.60	0.04
Other species	0.47		1.57	

*The RBA values were calculated from the data of Zavitkovski (Chap. 7, this volume); *Abies balsamea* was deleted.

area; i.e., each area was assumed to be in steady state relative to horizontal leaf movement. Deep depressions, which accumulated leaves, and smooth surfaces of large rocks, which shed leaves, were avoided as collecting sites. Since the extent to which leaves were transported by wind before reaching the ground is not known, we must assume that there may have been an exchange of leaves between study areas, probably in the direction of the prevailing wind. This movement was not documented, however.

Values of leaf-litter biomass reported here are considered to be underestimates of living foliage biomass. Viro (1955) found a 21% average loss in weight during yellowing of certain deciduous leaves prior to abscission. Leaves that fell before the end of the growing season undoubtedly underwent some decomposition, and some of these may have been excluded from sampling because they were confused with the previous year's litter fall. Furthermore, herbivory of both living and fallen leaves was not measured. Since inclusion of leaves produced during an earlier growing season would produce an overestimate of leaf biomass, considerable care was taken to avoid this error. In most cases leaves older than a few months were easy to recognize.

Finally, note that only deciduous leaves were collected. Needle leaves of the only conifer present in significant numbers, *Abies balsamea*, were not collected. This species accounted for 4.1 and 1.4% of total basal area in the aspen and maple–birch areas, respectively (Zavitkovski, Chap. 6, this volume).

RESULTS AND DISCUSSION

Total Annual Leaf-Litter Production

The amount of leaf litter that fell during 1971 in the aspen and maple–birch areas was within the range of 2 to 3 tonnes/ha, said by Tadaki (1966) to be typical for deciduous, broad-leaved forests (Table 1). The aspen area produced 2.32 tonnes/ha, and the maple–birch area produced 2.63 tonnes/ha, 13.4% more. These values are in close agreement with estimates based on monthly and twice-monthly litter-trap collections (Crow, Chap. 9, this volume). Leaf-litter production was lower in the midecotone, 1.79 tonnes/ha, probably because of the relatively low tree density (Murphy and Sharitz, Chap. 8, this volume).

In the aspen area 5.4% of the leaf litter was produced by shrub species; in the successionally more advanced maple–birch area, however, the shrub component of leaf litter accounted for only 2.7% of the total litter biomass. This difference may be related to the foliage density of the canopy. We had estimated the leaf-area index of the maple–birch canopy to be 5.5, significantly higher statistically than the value of 3.9 estimated for the aspen area (Murphy and Sharitz, Chap. 8, this volume). Shrub leaf-litter biomass may, therefore, be related to light availability in the understory.

Leaf-Litter Production by Individual Tree Species

Several different ways of describing forest composition on the basis of leaf litter were examined. The most interesting parameter was leaf-litter biomass per species as a percent of total leaf-litter biomass for the stand (relative leaf biomass). Relative leaf biomass was compared to relative basal area for each species (Table 2). For these comparisons the basal-area data of Zavitkovski (Chap. 6, this volume) were used because they are based on a total inventory of trees larger than 2.5 cm in diameter at breast height (dbh). Calculations showed that trees smaller than 2.5 cm dbh added a very small increment of basal area relative to larger trees. These basal-area data were available for the aspen and maple–birch areas but not for the midecotone. We deleted *A. balsamea* from Zavitkovski's total-stand basal-area data because the needle leaves of this conifer were not included in the litter samples.

The relation between relative basal area and relative leaf-litter biomass for tree species is presented in Fig. 1. In both the aspen and maple–birch areas, there is an approximate 1 : 1 relation between relative basal area and relative leaf-litter biomass. The statistically computed curves have slopes of 0.90 and 0.84 and correlation coefficients of 0.97 and 0.74 in the aspen and maple–birch areas, respectively. We must note that the correlation coefficient values tend to be inflated by the elongated patterns of the data points. Values of estimated relative error, as employed by Whittaker and Woodwell (1968), were high for both regressions, 0.43 for the aspen area and 0.78 for the maple–birch area. Nevertheless, in only one species in the aspen area and four in the maple–birch area did the

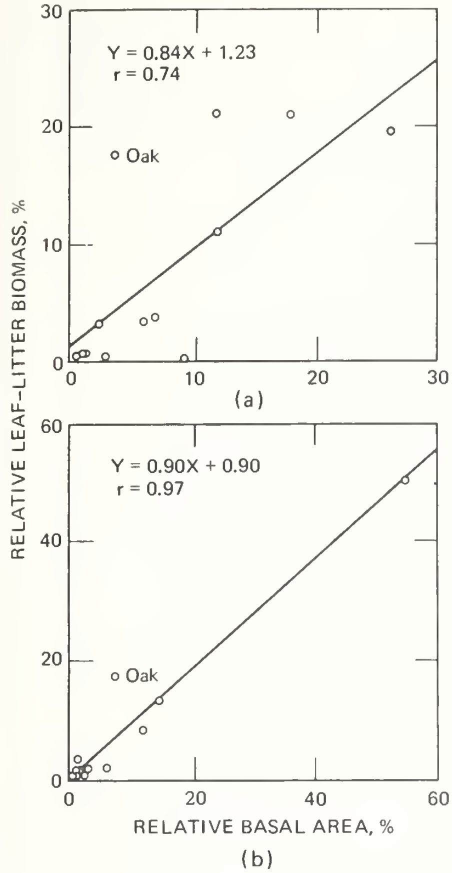

Fig. 1 Relation between relative leaf-litter biomass and relative basal area for trees in the maple–birch (a) and the aspen (b) forest types. r is the correlation coefficient.

Table 3

DIVERSITY OF LEAF LITTER IN THREE FOREST AREAS

Diversity index (based on leaves)	Aspen: Trees only	Aspen: Trees + shrubs	Midecotone: Trees only	Midecotone: Trees + shrubs	Maple–birch: Trees only	Maple–birch: Trees + shrubs
Number of species	12	16	13	15	14	16
Shannon–Weaver (ID)*						
Number basis	2.12	2.42	2.40	2.60	2.75	2.88
Biomass basis	2.25	2.47	2.50	2.65	2.73	2.84
Equitability (E)†						
Number basis	0.59	0.60	0.65	0.67	0.72	0.72
Biomass basis	0.63	0.62	0.68	0.68	0.72	0.71
Simpson's‡						
Number basis	0.62	0.68	0.75	0.78	0.82	0.84
Biomass basis	0.69	0.73	0.79	0.80	0.81	0.81

*ID = $-\Sigma\ p_i \log_2 p_i$, where p_i is the decimal fraction of total individuals or total biomass belonging to the *ith* species (Margalef, 1958).

†E = ID/$\log_2$ (number of species) (Pielou, 1969).

‡Simpson's diversity index = $1 - \Sigma_j[N_j(N_j - 1)]/N(N - 1)$, where N_j is the decimal fraction of total individuals or total biomass belonging to the *jth* species (Simpson, 1949).

values of relative basal area and relative leaf-litter biomass differ by more than 7%, and in no case was there a difference greater than 15%. Sampling error undoubtedly accounts for some of these differences, but in some species there is evidence that a 1 : 1 relation between relative basal area and relative foliage production does not exist (Zavitkovski, personal communication). For example, the ratio of crown volume to basal area tends to be larger for *Acer saccharum* and *Quercus rubra* than for *Populus tremuloides, Prunus serotina,* and *Fraxinus nigra.* The leaf-litter biomass of *Q. rubra,* the species showing the greatest discrepancy in both forest areas, may have been overestimated. Oak leaves decompose rather slowly, and some leaves from the previous year's growing season may have been included in the litter samples. The deletion of this species from the data increases the correlation coefficient from 0.74 to 0.85 in the maple–birch area and from 0.97 to 0.99 in the aspen area. Some of the scatter in the data points may have been caused by the litter sampling pattern. This consideration would apply to species that were clumped and were either close to or distant from the sample collection sites.

Reiners (1972) presented structural data, including basal area per species and foliage biomass per species, for three forest types in Minnesota, oak, fen, and cedar swamp. From his data we were able to calculate the relative basal area and relative foliage production for each tree species in each of the three forest types. In the oak and fen forest types, relative basal area differed from relative leaf biomass by no more than 5% in all species but two, and the maximum difference for any species was less than 10%. In the cedar swamp forest type, the values differed by more than 5% in only one species, and that difference was 7.79%.

Relations similar to those in Fig. 1 have been reported for comparisons of entire forest stands but not for comparisons of individual species within a stand. Bonnevie-Svendsen and Gjems (1957) observed larch, Norway spruce, Scotch pine, and beech stands in Norway and found a relation between forest-stand basal area and leaf production. Leaf-litter fall averaged about 70 to 75 kg/m^2 of basal area over a basal-area range of 8 to 40 m^2/ha. In the present study of a deciduous forest, the ratio of leaf-litter production to basal area was found to be considerably higher averaging 134 kg/m^2 in the aspen area and 142 kg/m^2 in the maple–birch area (oven-dry weight).

Diversity of Leaf Litter

Three indexes of species diversity were calculated for the leaf-litter samples, Simpson's index, the Shannon–Weaver index (ID), and an equitability index (E). Diversity was calculated on the basis of number of leaves per species and biomass of leaves per species. A summary of the diversity values, for trees and shrubs pooled and for trees only, is presented in Table 3.

In determining an adequate sample size for diversity estimates based on leaf litter, we found that one 0.25-m^2 sample yielded the same diversity (±0.2) as four such plots pooled when the four samples were taken from within 1 m of each other. But when all 20 samples from within one forest area separated by distances of up to 40 m were pooled, a larger diversity value consistently resulted. Diversity estimates based on the pooling of 20 samples differed by less than 0.1 from estimates based on only 12 pooled samples. The values in Table 3 are based on the pooled data from 20 samples, each 0.25 m^2 in area, from each forest area.

All indexes indicate that leaf diversity is lowest in the aspen area, intermediate in the midecotone, and highest in the maple–birch area. This relationship can be attributed partly to the number of species in each area and partly to equitability, which is greatest in the maple–birch area and lowest in the aspen area. The same pattern in diversity occurs

regardless of whether the values are based on numbers of leaves or on biomass of leaves. In the aspen area and midecotone, the distribution of biomass of leaves across species is more uniform than the distribution of numbers of leaves, as indicated by the higher diversity and equitability values for leaf litter calculated on a biomass basis. In the maple–birch area, the diversities based on biomass and numbers are almost identical.

The differences in diversity between forest types are similar regardless of whether whole trees or leaves are used as the basis for calculation. Murphy and Sharitz (Chap. 8, this volume) reported ID values of 1.41, 2.08, and 2.53 for trees 2.5 cm or more in dbh in the aspen, midecotone, and maple–birch areas, respectively. These diversity estimates were based on a sampling of 110 m^2 in each area. Zavitkovski (Chap. 6, this volume), who inventoried all trees within 50 m of the radiation source in the aspen and maple–birch areas, reported ID values of 2.35 and 3.18, respectively.

Reference to Chap. 8, by Murphy and Sharitz, shows that diversity patterns in the sapling and seedling strata are somewhat different than would be predicted by analysis of leaf litter or canopy trees. The greatest diversity of saplings was found in the midecotone and the greatest diversity of seedlings was found in the aspen area. The contribution of seedlings and saplings to leaf litter is very small relative to canopy trees. Thus leaf-litter diversity patterns closely approximate canopy diversity patterns but indicate very little about the composition of the understory.

In recent years the concept of diversity has received considerable attention in the ecological literature. There has been much speculation and debate about the best way to calculate and interpret indexes of diversity. We should note that Simpson's index and the Shannon–Weaver index responded in approximately the same way to the data evaluated in this study. The Shannon–Weaver index, which is popular at the moment, is more difficult to calculate than Simpson's index and is not necessarily more useful. Both indexes are influenced by equitability as well as variety. In most studies, including this one, the diversity values are useful for comparative purposes primarily and the absolute values are of limited interest in themselves.

SUMMARY AND CONCLUSIONS

Annual leaf-litter production of 1971 in the aspen- and maple–birch-dominated areas of the Enterprise Forest was within the range of 2 to 3 tonnes/ha. These estimates are in accord with values reported in the literature for similar types of deciduous forests. The fraction of leaf litter produced by shrubs was lowest in the maple–birch area and greatest in the early-successional aspen area, although in no area did shrub leaf litter account for more than 6% of total leaf litter. The differences in shrub contribution between areas may be related to canopy foliage density, as suggested by an inverse relation between shrub leaf-litter production and forest leaf-area index.

An approximate 1 : 1 relation appears to exist between relative leaf-litter production per tree species and relative basal area per tree species. In most species the percent of total-stand basal area contributed was similar to the percent of total leaf litter contributed. Certainly more data need to be collected to further test and refine the relationship, especially in other forest types. The data of Reiners (1972) for oak, fen, and cedar swamp forest types fit the relationship rather well.

Indexes of species diversity, whether based on leaf biomass or leaf numbers per species, yielded similar relationships. Both the Shannon–Weaver values and Simpson's values indicated that the maple–birch area is most diverse and the early-successional aspen area is least diverse. This result agrees with the studies of canopy diversity based on numbers of trees per species. The absolute index values vary depending on the unit measured or counted, but the degree of difference between forest areas was similar in all cases.

These preliminary findings indicate that descriptions of deciduous-forest canopy composition, whether based on the analysis of leaf litter or of whole trees, are essentially parallel. Further studies in other types of deciduous forests, including those representing different seral stages, are planned. Previous studies in other forests have shown relations between total-stand basal area and total leaf-litter production. It may, therefore, be possible to estimate the whole-tree biomass of selected species within the forest array from analysis of leaf litter, although the method would not necessarily be easier than traditional methods. The relations between leaf-litter production and basal area presented in this chapter would have to be correlated with information relating the basal area of trees to their biomass. Dimension analysis has already provided this type of information for some forest types.

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Vertebrates of the Enterprise Forest: A General Survey

11

RICHARD R. BUECH
Institute of Forest Genetics, North Central Forest Experiment Station, Forest Service, U. S. Department of Agriculture, Rhinelander, Wisconsin

ABSTRACT

Studies of the effects of gamma radiation on northern forest ecosystems are in progress at the Enterprise Forest in northern Wisconsin. This paper presents a separate species list for four classes of vertebrates, Amphibia, Reptilia, Aves, and Mammalia, found in the radiation forest. The lists will benefit people with specific interest in suitable study material for subsequent radiation experiments as well as those with a general interest in the vertebrate fauna of the area. The lists range from accurate for mammals to incomplete for avian forms.

That the Enterprise Forest is within the glacial drift area of northern Wisconsin is clearly manifest in the variable soils and topography of the area. These factors, in conjunction with more recent vegetational modifiers, such as fire and logging, have resulted in a great interspersion of vegetational types. The variety and interspersion of forest and bog habitats and the remoteness of the area contribute to a diversity of vertebrate species not otherwise possible in such a relatively small area.

AMPHIBIA

Conant (1958) shows seven species of urodeles as having ranges that include the Enterprise Forest (Table 1). Of these, three have been identified in the area. The most common species is the terrestrial red-backed salamander (*Plethodon cinereus*), which belongs to the family of lungless salamanders (Plethodontidae). The other two are mole salamanders belonging to the family Ambystomidae. These two species, the spotted salamander (*Ambystoma maculatum*) and the blue-spotted salamander (*A. laterale*), are observed less frequently.

Table 1

TENTATIVE LIST* OF AMPHIBIAN SPECIES IN THE ENTERPRISE FOREST

Order	Family	Genus and species	Common name
Urodela	Proteidae	*Necturus maculosus*	Mud puppy
	Ambystomidae	*Ambystoma jeffersonianum*	Jefferson salamander
		A. laterale	X Blue-spotted salamander
		A. maculatum	X Spotted salamander
	Salamandridae	*Diemictylus viridescens*	Central newt
	Plethodontidae	*Plethodon cinereus*	X Red-backed salamander
		Hemidactylium scutatum	Four-toed salamander
Anura	Bufonidae	*Bufo americanus*	X American toad
	Hylidae	*Hyla crucifer*	X Northern spring peeper
		H. versicolor	Eastern gray tree frog
		Pseudacris triseriata maculata	Boreal chorus frog
		P. t. triseriata	Western chorus frog
	Ranidae	*Rana catesbeiana*	Bullfrog
		R. septentrionalis	Mink frog
		R. clamitans	X Green frog
		R. pipiens	X Northern leopard frog
		R. palustris	Pickerel frog
		R. sylvatica	X Wood frog

*The list was compiled from range maps of amphibians listed by Conant (1958). Species actually observed in the area are marked with an X.

Conant shows eleven species of anurans as having ranges that include the Enterprise Forest (Table 1), one bufonid, four hylids, and six ranids. Of these, five species have been observed. The American toad (*Bufo americanus*) is common in a variety of habitats. Of the four hylids only one, the northern spring peeper (*Hyla crucifer*), has been observed to date. The ranid species identified are the green frog (*Rana clamitans*), the wood frog (*R. sylvatica*), and the northern leopard frog (*R. pipiens*). All but the northern leopard frog are fairly common over much of the area. All these anurans may be seen frequently during the warmer months, but they are most noticeable during late April and May, when they congregate in small swamps for breeding. At this time their vocalizations can hardly go unnoticed. A number of breeding ponds in site 1 are actively used each year. All are temporary because the standing water in most disappears by late summer.

REPTILIA

Table 2 outlines the probable occurrence of reptilian forms following the range maps of Conant (1958) for the Enterprise Forest. One skink (*Eumeces fasciatus*) is listed, but no skinks have been observed.

The eight snake species shown by Conant as having ranges that include the Enterprise Forest belong to the family Colubridae. Five species have been ob-

served: the northern red-bellied snake (*Storeria occipitomaculata*), the eastern smooth green snake (*Opheodrys vernalis*), the northern ring-necked snake (*Diadophis punctatus*), the western fox snake (*Elaphe vulpina*), and the eastern garter snake (*Thamnophis sirtalis*). The garter snake is by far the most widely occurring species and is common in site 1. The remaining three species listed by Conant have not been sighted in this area, and it is probable that the bull snake (*Pituophis melanoleucus*) does not live in this forest since it prefers habitats not present in the area.

Table 2

TENTATIVE LIST* OF REPTILE SPECIES IN THE ENTERPRISE FOREST

Order	Family	Genus and species	Common name
Squamata	Scincidae	*Eumeces fasciatus*	Five-lined skink
	Colubridae	*Natrix sipedon*	Northern water snake
		Storeria occipitomaculata	X Northern red-bellied snake
		Thamnophis sirtalis	X Eastern garter snake
		Heterodon platyrhinos	Eastern hognose snake
		Diadophis punctatus	X Northern ring-necked snake
		Opheodrys vernalis	X Eastern smooth green snake
		Elaphe vulpina	X Western fox snake
		Pituophis melanoleucus	Bull snake
Chelonia	Chelydridae	*Chelydra serpentina*	Snapping turtle
	Testudinidae	*Clemmys insculpta*	Wood turtle
		Chrysemys picta belli	X Western painted turtle
		C. p. marginata	Midland painted turtle
		Emydoidea blandingi	Blanding's turtle
	Trionychidae	*Trionyx spinifer*	Eastern spiny soft-shelled turtle

*The list was compiled from range maps of reptiles listed by Conant (1958). Species actually observed in the area are marked with an X.

AVES

Eleven species of birds that are year-round residents have been observed in the forest; several other species are either seasonally resident or migrate through the area. Those which migrate were eliminated from this discussion since they are transitory, are infrequently observed, and are unsuitable subjects for radiation studies in the area.

Year-round residents include the ruffed grouse (*Bonasa umbellus*), which is common and was hunted through the fall of 1970. In the spring of 1971, when the fence was completed, the area was made inaccessible to hunters. Although more abundant during the winter, the raven (*Corvus corax*) is also present year-round. Other permanent residents include the great horned owl (*Bubo virginianus*), the barred owl (*Strix varia*), the blue jay (*Cyanocitta cristata*), the black-capped chickadee (*Parus atricapillus*), the white-breasted nuthatch (*Sitta carolinensis*), the purple finch (*Carpodacus purpureus*), and three picid species, the pileated woodpecker (*Dryocopus pileatus*), the hairy woodpecker (*Dendrocopus villosus*), and the downy woodpecker (*D. pubescens*). All are common except the pileated woodpecker and the two owls, which are seen only occasionally.

In addition to these permanent residents, the following species are present during the winter: the Canada jay (*Perisoreus canadensis*), the evening grosbeak (*Hesperiphona vespertina*), the redpoll (*Acanthis flammea*), the pine siskin (*Spinus pinus*), and the snow bunting (*Plectrophenax nivalis*). The list of numerous summer residents (included in Table 3) is the one most likely to be incomplete. Perhaps the most common of those listed is the robin (*Turdus migratorius*).

MAMMALIA

The mammalian species in the Enterprise Forest were identified from sightings, from sign, and, in the case of small mammals, from live- and snap-trap programs conducted from 1968 to 1972. Before the 8-ft-high cyclone fence was completed, the large mammal populations were what might be expected given the habitat provided by an area of this size (1440 acres). Since its completion, the fence has altered ingress and egress patterns for some of the larger species. As a result, the frequency of occurrence of some animals has been reduced, if not eliminated altogether. Table 4 lists species that have been or are present in the forest. To date 30 species representing 15 families have been identified. For a more comprehensive discussion of the small mammals, see Chap. 12, this volume.

Four insectivores are present, three soricids and one talpid. The most common soricid, and at times the most abundant small mammal, is the short-tailed shrew (*Blarina brevicauda*). The arctic shrew (*Sorex arcticus*) is present but is rarely captured; for every one of these, three masked shrews (*Sorex cinereus*) were taken. Sign of the sole talpid, the star-nosed mole (*Condylura cristata*), is infrequently observed.

The red bat (*Lasiurus borealis*) was the only vespertilionid observed. Other species are probably present, but no systematic effort was made to collect them.

One leporid, the snowshoe hare (*Lepus americanus*), is present in the vicinity of coniferous lowlands and was abundant during the winter of 1971–1972.

Fourteen species of rodents, representing five families, are present: five sciurids, five cricetids, one murid, two zapodids, and one erethizontid. The sciurids include two species of chipmunk, the eastern chipmunk (*Tamias striatus*) and the least chipmunk (*Eutamias minimus*). Although they are sympatric species, it is doubtful that the two populations of chipmunks intermingle extensively here since the larger eastern chipmunk tends to occupy the more deciduous habitats. The other sciurid species present are the gray squirrel (*Sciurus carolinensis*), the red squirrel (*Tamiasciurus hudsonicus*), and the flying squirrel (*Glaucomys sabrinus*). The gray squirrel is not particularly abundant, perhaps because of the species composition of the deciduous forest cover. The red squirrel is common where conifers are abundant. Little is known about the abundance of flying squirrels since they are nocturnal animals, but a few were trapped or observed in the daylight hours during the breeding season.

Representative of the cricetids are two cricetines, the woodland deer mouse (*Peromyscus maniculatus gracilis*) and the white-footed mouse (*P. leucopus noveboracensis*), and three microtines, the bog lemming (*Synaptomys cooperi*), the red-backed vole (*Clethrionomys gapperi*), and the meadow vole (*Microtus pennsyl-*

Table 3

TENTATIVE LIST OF AVIAN SPECIES IN THE ENTERPRISE FOREST

Family	Genus and species	Common name	Seasonal presence*
Ardeidae	*Ardea herodias*	Great blue heron	3
Accipitridae	*Buteo jamaicensis*	Red-tailed hawk	3
	B. platypterus	Broad-winged hawk	3
	Circus cyaneus	Marsh hawk	3
Tetraonidae	*Bonasa umbellus*	Ruffed grouse	1,4
Scolopacidae	*Philohela minor*	Woodcock	3,4
Columbidae	*Zenaidura macroura*	Mourning dove	3
Strigidae	*Bubo virginianus*	Great horned owl	1
	Strix varia	Barred owl	1
Trochilidae	*Archilochus colubris*	Ruby-throated hummingbird	3
Picidae	*Colaptes auratus*	Flicker	3,4
	Dryocopus pileatus	Pileated woodpecker	1
	Sphyrapicus varius	Yellow-bellied sapsucker	3,4
	Dendrocopus villosus	Hairy woodpecker	1
	D. pubescens	Downy woodpecker	1
Tyrannidae	*Sayornis phoebe*	Eastern phoebe	3
Hirundinidae	*Iridoprocne bicolor*	Tree swallow	3
Corvidae	*Perisoreus canadensis*	Canada jay	2
	Cyanocitta cristata	Blue jay	1,4
	Corvus corax	Raven	1
	C. brachyrhynchus	Crow	3
Paridae	*Parus atricapillus*	Black-capped chickadee	1
Sittidae	*Sitta carolinensis*	White-breasted nuthatch	1
Certhiidae	*Certhia familiaris*	Brown creeper	3
Mimidae	*Dumetella carolinensis*	Catbird	3
	Toxostoma rufum	Brown thrasher	3
Turdidae	*Turdus migratorius*	Robin	3,4
	Hylocichla guttata	Hermit thrush	3,4
Vireonidae	*Vireo olivaceus*	Red-eyed vireo	3,4
Parulidae	*Mniotilta varia*	Black-and-white warbler	3
	Parula americana	Parula warbler	3
	Dendroica petechia	Yellow warbler	3
	D. virens	Black-throated green warbler	3
	Seiurus aurocapillus	Ovenbird	3,4
	Geothlypis trichas	Yellowthroat	3
Icteridae	*Agelaius phoeniceus*	Red-winged blackbird	3
	Icterus galbula	Baltimore oriole	3
	Molothrus ater	Brown-headed cowbird	3,4
Fringillidae	*Pheucticus ludovicianus*	Rose-breasted grosbeak	3
	Hesperiphona vespertina	Evening grosbeak	2
	Carpodacus purpureus	Purple finch	1
	Acanthis flammea	Redpoll	2
	Spinus pinus	Pine siskin	2
	S. tristis	Common goldfinch	3
	Zonotrichia albicollis	White-throated sparrow	3
	Melospiza melodia	Song sparrow	3
	Plectrophenax nivalis	Snow bunting	2

*Seasonal presence codes are: 1, permanent resident, observed in the area in all seasons; 2, winter visitor, observed in the area only during the winter; 3, summer visitor, observed only during the summer; and 4, nesting observed.

vanicus). The two species of *Peromyscus* are common, are sympatric, and their populations are seemingly intermingled. The bog lemming is relatively rare in comparison to the red-backed vole. The meadow vole is common in grassy areas, but, since grassy habitat is infrequent in the forest, they are probably fewer than the bog lemming in terms of total numbers.

The sole murid species, the Norway rat (*Rattus norvegicus*), was represented by one individual. This was probably a freak occurrence and not representative of a resident population.

The two zapodids, the meadow jumping mouse (*Zapus hudsonius*) and woodland jumping mouse (*Napaeozapus insignis*), are both infrequently observed. The remaining rodent, the porcupine (*Erethizon dorsatum*), is common in the forest and is particularly abundant in certain localities.

Nine species of carnivores, representing five families, frequent the forest or are residents. Two canids, the coyote (*Canis latrans*) and the red fox (*Vulpes fulva*), were observed in the area before it was fenced, but, in the winter following fence closure (1971–1972), they were absent. It seems, however, that the fence will prevent ingress–egress movement for those two species only during periods of deep snow cover.

The black bear (*Euarctos americanus*) is an occasional "visitor." Surprisingly the fence presented no obstacle to the entry of a pair of bears during 1971. Tracks revealed that they approached the fence directly and dug their way underneath, without any lateral movement along the fence at all. The raccoon (*Procyon lotor*) is common, as are the skunk (*Mephitis mephitis*) and the short-tailed weasel (*Mustela erminea*), although populations of the latter apparently declined before the winter of 1971–1972. The remaining carnivores, the fisher (*Martes pennanti*), the mink (*Mustela vison*), and the bobcat (*Lynx rufus*), are rare; there was only one sign or sighting of each.

Before the winter of 1971–1972, the white-tailed deer (*Odocoileus virginianus*) was a common resident during the snow-free period. During periods of heavy snow cover, however, it was present only on the peripheral northern edges of the area. The impact of a protected, enclosed population of deer on vegetation of the experimental area was considered incompatible with the objectives of the planned studies. To avoid the necessity of continuing population control measures, the population of deer was removed entirely from within the 1440-acre enclosure during the winter of 1971–1972. Four live traps baited with hay were operated from Jan. 5 to Mar. 31, 1972, for a total of 247 trap nights. The final removal was accomplished by shooting, during Mar. 21 to 31, 1972. A total of 36 deer (16.0/sq mile) were removed from the area (Table 5), 22 by live trapping, 11 by shooting, and 3 by miscellaneous means. Of the total, 28 were adults (an adult was defined as being at least 1 year old) and 8 were fawns. Of the 28 adults, 9 were male, 17 were female, and 2 were of undetermined sex. Of the 8 adult females shot, 7 were examined for presence of fetuses. All 7 were found to be carrying at least 1 fetus, and 3 were carrying twins; thus an average of 1.43 fetuses per adult doe was found.

These statistics are similar to those given by Dahlberg and Guettinger (1956) for deer in Wisconsin with the following exceptions: The fawn component of the

total herd removed was less than expected according to the prehunting-season average herd composition of 18% bucks, 43% does, and 39% fawns reported by Dahlberg and Guettinger. However, they believed their percentages may have overestimated the antlerless components of the herd. Also, although no instance of natural mortality was encountered in the forest, the herd composition we obtained is more accurately described as late winter rather than prehunting season, to which it is compared. It is also probable that the deer density figure of 16/sq mile was somewhat inflated because of a concentration of deer activity on the recently cleared fence line at the time of fence closure.

DISCUSSION

Although there is seemingly a wide choice of vertebrates in which to observe radiation effects, various considerations, such as species density, range of individual activity with respect to a point radiation source, and sensitivity of the end point being measured, limit intensive studies to the more numerous sedentary species.

Vertebrate studies presently being conducted include an intensive investigation of radiation effects on small mammals and observations of avian nesting success in the vicinity of the radiation source. Future investigations might include more intensive studies of nesting avifauna or studies of the effects of radiation on such amphibians as *P. cinereus, H. crucifer*, and *R. sylvatica* or such reptiles as *T. sirtalis*. Success in demonstrating radiation effects may well depend on the end point being observed. If the end point used is mortality, severe restrictions are imposed on the selection of a species to be observed because of the relatively small area around a 10,000-Ci ^{137}Cs point radiation source where doses significant to an individual's survival are obtained. A more useful end point would be some physiologically measurable state of health of the individual which is sensitive at sublethal dose levels. This would effectively increase the area about the source where radiation effects can be observed. Finally, consideration must be given to the habitat provided by future radiation sites, the season during which exposure is to occur, the duration of the exposure, etc.

Table 4

TENTATIVE LIST OF MAMMAL SPECIES IN THE ENTERPRISE FOREST

Family	Genus and species	Common name
Soricidae	*Sorex cinereus*	Masked shrew
	S. arcticus	Arctic shrew
	Blarina brevicauda	Short-tailed shrew
Talpidae	*Condylura cristata*	Star-nosed mole
Vespertilionidae	*Lasiurus borealis*	Red bat
Leporidae	*Lepus americanus*	Snowshoe hare
Sciuridae	*Tamias striatus*	Eastern chipmunk
	Eutamias minimus	Least chipmunk
	Sciurus carolinensis	Gray squirrel
	Tamiasciurus hudsonicus	Red squirrel
	Glaucomys sabrinus	Flying squirrel
Cricetidae		
Subfam. Cricetinae	*Peromyscus maniculatus gracilis*	Woodland deer mouse
	P. leucopus noveboracensis	White-footed mouse
Subfam. Microtinae	*Synaptomys cooperi*	Bog lemming
	Clethrionomys gapperi	Red-backed vole
	Microtus pennsylvanicus	Meadow vole
Muridae	*Rattus norvegicus*	Norway rat
Zapodidae	*Zapus hudsonius*	Meadow jumping mouse
	Napaeozapus insignis	Woodland jumping mouse
Erethizontidae	*Erethizon dorsatum*	Porcupine
Canidae	*Canis latrans*	Coyote
	Vulpes fulva	Red fox
Ursidae	*Euarctos americanus*	Black bear
Procyonidae	*Procyon lotor*	Raccoon
Mustelidae	*Martes pennanti*	Fisher
	Mustela erminea	Short-tailed weasel
	M. vison	Mink
	Mephitis mephitis	Skunk
Felidae	*Lynx rufus*	Bobcat
Cervidae	*Odocoileus virginianus*	White-tailed deer

Table 5

SUMMARY BY SEX AND AGE OF DEER REMOVED FROM THE ENTERPRISE FOREST

Means of removal	Age	Number of males	Number of females	Number of unknown sex	Total
Live trapping	Adult	6	9		15
	Fawn		6	1	7
Shooting	Adult	3	8		11
Miscellaneous	Adult			2	2
	Fawn			1	1
Total		9	23	4	36

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Small-Mammal Populations in Site 1 and the Control Area

12

RICHARD R. BUECH
Institute of Forest Genetics, North Central Forest Experiment Station, Forest Service, U. S. Department of Agriculture, Rhinelander, Wisconsin

ABSTRACT

*A live-trap study of small-mammal populations and their response to gamma radiation is in progress in the Enterprise Radiation Forest near Rhinelander, Wisconsin. Trapping in northern forest communities has been conducted on a monthly basis since May 1970, along two grids totaling 8.9 ha in size. Data gathered from the two grids before radiation treatment were combined to present information concerning the trappability, populations, reproduction, and body weight of the most prominent species. Species studied are the red-backed vole (*Clethrionomys gapperi*), the short-tailed shrew (*Blarina brevicauda*), the eastern chipmunk (*Tamias striatus*), the meadow vole (*Microtus pennsylvanicus*), the woodland deer mouse (*Peromyscus maniculatus gracilis*), and the white-footed mouse (*P. leucopus*).*

Chapter 11, this volume, lists the mammalian species found in the Enterprise Forest. For site 1 and the control area, the list can be reduced by considering only the more common species. This leaves one soricid, the short-tailed shrew (*Blarina brevicauda*), and five rodents, the eastern chipmunk (*Tamias striatus*), the woodland deer mouse (*Peromyscus maniculatus gracilis*), the white-footed mouse (*P. leucopus noveboracensis*), the red-backed vole (*Clethrionomys gapperi*), and the meadow vole (*Microtus pennsylvanicus*). On the basis of sampling conducted before gamma-radiation treatment, these six will probably be the most important species in the radiobiology studies conducted in site 1 and the control area. Accordingly only information about these common species is presented here.

The study of small mammals and their populations is directed toward determining: (1) the influence of radiation-induced vegetational changes on small-mammal species composition, (2) the influence of radiation per se on the distribution of small mammals, and (3) the influence of radiation on the dynamics of small-mammal populations.

Some general aspects of the biology and populations of the species previously mentioned are provided as a reference against which future treatment and post-treatment observations can be compared. For this purpose, pretreatment data for both areas were combined to present information with regard to populations, reproductive activity, and body weights. Comparisons among areas and among data collected before, during, and after radiation treatment are to be reported at a later date. For purposes of our general discussion, *P. maniculatus gracilis* and *P. leucopus noveboracensis* were lumped together as *Peromyscus* sp. Floristic and physical descriptions of site 1 and the control area can be found elsewhere in this volume.

METHODS

Circular live-trapping grids with 15-m station intervals were established in site 1 and the control area. Circular grids were employed because of the configuration of radiation about a point source. A secondary benefit is that a circle has the smallest perimeter relative to its area. The treatment grid encompassed an area of approximately 6.2 ha with a radius of 135 m; the control grid had an area of 2.7 ha with a radius of 90 m. See Chap. 2, this volume, for more-detailed descriptions of the grids.

Each grid station was supplied with a trap shelter described by Iverson and Turner (1969), modified in dimension and material to accommodate a small-mammal live trap that I designed for year-round use. The shelters were used year-round to protect the traps under the snow in the winter and to shade the traps in other seasons. Peanut butter and rolled oats in ¾-oz portion-control cups provided food, and an apple slice provided a source of water. Details of the trap and trapping techniques have been described by Buech (in preparation).

Trapping was conducted for a 5-day period each month from May 1970 to April 1972. Table 1 outlines the specific dates that both areas were trapped. Every fourth grid station was provided with a trap for one trap night each month, and the traps were rotated so that in a 4-night trapping period each grid station held a trap for one night. One hundred one traps were used the first trap night, and 99 were used for the remaining trap nights. This resulted in a monthly sample of 277 trap nights for the site 1 grid and 121 for the control grid. Traps were baited and set on Monday morning and remained set until Friday, when bait was removed and they were locked shut. Each trap was checked once every 24 hr, and at this time its location was advanced one grid station. When these procedures were followed, rodent trap mortality was minimal.

Upon first capture all species except chipmunks were toe clipped for identification. In addition, all species except shrews and voles were ear tagged with numbered Monel-metal fingerling-fish tags. At first capture during a given trapping period, we recorded the follow-

ing data for all mammals: identification number, species, grid location, day and week number, weight, and sex. For females we also recorded vagina perforate or not perforate; nipples small, medium, or large; and pubic symphyses closed, slightly open, or open; and for males, testes position, scrotal or abdominal. For subsequent captures during a given trapping period, only the identification number, species, grid location, and day number were recorded. Animals were weighed and released at the trap location. Ohaus Scale Corporation Model 8010 and 8011 dial-type spring scales were used, and readings were obtained to the nearest gram.

Data were punched on IBM cards using the format and programs described by Krebs (1967). Programs were modified to accept data for a number of different species and to accommodate slight variations in sampling procedure. Only a portion of the data, that pertaining to populations, reproductive activity, and body weights, has been processed.

Some of the programs classify individuals as to age class (adult, subadult, and juvenile) on the basis of body weight. This required us to establish body-weight limits for the three age classes. For seasonally breeding populations at least, this posed a problem since reproductively active adults showed weight losses as they became reproductively quiescent during winter; i.e., their body weight descended to that of a subadult. Thus there are some inherent ambiguities of weight classification which must be taken into account when this information is used for interpretive purposes. The limits used were based on a study of individual weight histories, reproductive information, and body-weight distributions. For purposes of this study, weight limits were set so that the juvenile class would include only the very young. The weight selected to divide the juvenile and subadult classes was set low enough to exclude from the juvenile class, as much as possible, overwintering individuals who had lost weight. The weight selected to divide the subadult and adult classes was set so that the adult class would include only mature, reproductively active individuals. Thus the subadult class contained young of the year who were nearly adult size but generally not reproductively active, and during the winter it also included adults who were at this time reproductively inactive.

Table 1

WEEKLY PERIODS DURING WHICH TRAPPING WAS CONDUCTED IN SITE 1 AND THE CONTROL AREA FROM MAY 1970 TO APRIL 1972

Week number*	Dates trapped	Dates trapped, year days
20	May 18-22, 1970	138-142
24	June 15-19, 1970	166-170
29	July 20-24, 1970	201-205
33	Aug. 17-21, 1970	229-233
37	Sept. 14-18, 1970	257-261
41	Oct. 12-16, 1970	285-289
46	Nov. 16-20, 1970	320-324
50	Dec. 14-18, 1970	348-352
54	Jan. 11-15, 1971	11-15
59	Feb. 15-19, 1971	46-50
63	Mar. 15-19, 1971	74-78
67	Apr. 12-16, 1971	102-106
72	May 17-21, 1971	137-141
76	June 14-18, 1971	165-169
81	July 19-23, 1971	200-204
85	Aug. 16-20, 1971	228-232
89	Sept. 13-17, 1971	256-260
94	Oct. 18-22, 1971	291-295
98	Nov. 15-19, 1971	319-323
102	Dec. 13-17, 1971	347-351
106	Jan. 10-14, 1972	10-14
111	Feb. 14-18, 1972	45-49
115	Mar. 13-17, 1972	73-77
119	Apr. 10-14, 1972	101-105

*Weeks were numbered consecutively beginning with Jan. 4-10, 1970, which was designated as week 1.

The weight-class limits were set as follows:

Species	Weight, g Juvenile	Subadult	Adult
Tamias striatus	<76	76 to 96	>96
Peromyscus sp.	<16	16 to 21	>21
Clethrionomys gapperi	<14	14 to 19	>19
Microtus pennsylvanicus	<20	20 to 29	>20
Blarina brevicauda	<13	13 to 15	>13

Methods of quantifying the physical and vegetational characteristics of the grid locations and dosimetry methods for individual animals will be reported later when data collection is complete.

RESULTS AND DISCUSSION

Trappability

No effort is made here to estimate the total size of the populations of various species present at any given point in time. We report numbers of individuals known to be alive during a given period which belong to the "trappable" portion of the population. For the sake of simplicity, this number is hereafter referred to as the "population" although it is in actuality some changing fraction of the true total population. For various reasons some animals, especially individuals living on the periphery, may not be captured during a given trapping period but are captured during subsequent periods. Thus the number of individuals known to be alive include those known to have skipped capture during the period in question. Also a distinction is made as to the trappable portion of the population because some, especially the very young, are present but not trappable.

As an indication of the effectiveness of the sampling procedures and equipment used in enumerating populations of the species under consideration, Table 2 estimates the trappability, i.e., the number of animals captured expressed as a percent of those known to be alive during a given sampling period summed over the periods indicated (Krebs, Keller, and Tamarin, 1969). With the possible exception of *Blarina*, trappability of all species was notably less during the winter of 1970–1971. That the species were less trappable may have been a manifestation

of the larger number of individuals per available trap. Relatively speaking, we can see that *Clethrionomys* and *Peromyscus* were both more readily captured than *Blarina, Microtus*, or *Tamias*. On the average about 90% of the resident trappable populations of *Clethrionomys* and *Peromyscus* was enumerated during a given sampling week. For *Blarina* trappability was related to the number of animals captured; i.e., it was greatest during periods of higher populations (up to 96%, N = 46, N is the number of individuals known to be alive at the time). *Microtus* was apparently less prone to capture during periods when snow cover was present than during the snow-free period. For *Tamias* trappability was for the most part greater than 70%. Thus, with repeated sampling on a monthly basis, we arrived at a reasonably accurate estimate of population fluctuations.

Populations

Clethrionomys gapperi. Figure 1 shows by species the minimum number of animals known to be alive in both site 1 and the control area from May 1970 to April 1972. During this period the *Clethrionomys* population increased in 1970 and decreased in 1971. Their population was at a low point when trapping began in May 1970 but increased rapidly until October. It peaked in December 1970 and then began a decline that was only partially abated during the 1971 breeding season. The decline intensified by September 1971, and the population dropped to a low in January 1972 which was maintained throughout the winter of 1972.

On the basis of the highest population observed (December 1970), 4.7 individuals per hectare (1.9/acre) were found, assuming a combined grid size of 8.9 ha. This figure approaches the maximum estimate expected for the trappable portion of the December 1970 population (no effort was made to estimate the effective area of the grid). In a northern Michigan study, Manville (1949) compensated for the effective grid area and arrived at a similar maximum density of 1.1/acre on his plot number 4, which most closely approximates the habitat in the Enterprise study area. Buckner (1957) also reported a maximum density of 1.1/acre in a black spruce–tamarack stand.

Peromyscus sp. The capture data indicate that *Peromyscus* undergoes an annual cycle of increase and decrease in population (Fig. 1). The population was at a low when trapping was initiated in May 1970. A rapid increase occurred until a peak was reached in August and September 1970. The population then declined until November, dropped rapidly with the advent of snow cover in December 1970, and then declined slowly through the winter to a low in March 1971. During the 1971 breeding season, the population increased irregularly to a high in August which was only half that of the previous year. A slow decline occurred until November and then intensified during the winter of 1972 until a low was reached in March and April.

Maximum density during the study, in August and September 1970, was determined to be 5.4 individuals per hectare (2.2/acre), assuming a grid size of 8.9 ha. This is considerably short of the 11.0/acre maximum found by Manville (1949) in northern Michigan. However, data reviewed by Terman (1968) indicates that 11.0/acre may be an exceptionally high density.

Blarina brevicauda. The population of *Blarina* is more difficult to assess with certainty because of inevitable mortality. During any given sampling period, an average of 65% (or 55% of those known to be alive) were lost to trap mortality. Thus the sampling procedure had a harvesting aspect to it. In Fig. 1 the shaded area under the curve of animals known to be alive represents animals lost to trap mortality. We can only speculate what influence the harvest had on subsequent immigration and recruitment from within the study area itself. The expectation is that it increased immigration and decreased recruitment. In this discussion we assume that the 1-month interval between harvests allowed populations in the study area to approach those of the surrounding unharvested areas for assessment of population trends. One other qualification that bears mentioning is a possibility of density-dependent and/or seasonal bait attractiveness. This possibility is suggested by the trappability data provided in Table 2, where trappability was greatest during periods of snow cover and of higher population densities.

The population trends for *Blarina* indicate that very low numbers were present when trapping began in May

Table 2

TRAPPABILITY* OF *Clethrionomys gapperi*, *Peromyscus* SP., *Blarina brevicauda*, *Microtus pennsylvanicus*, AND *Tamias striatus* IN THE SITE 1 AND CONTROL GRIDS COMBINED

Period	Number of months	*Clethrionomys gapperi*		*Peromyscus* sp.		*Blarina brevicauda*		*Microtus pennsylvanicus*		*Tamias striatus*	
		N	T	N	T	N	T	N	T	N	T
May–June 1970	2	16	100.0	12	100.0			3	66.7	8	87.5
July–Nov. 1970	5	154	91.6	199	89.4	22	68.2	12	91.7	86	75.6
Dec. 1970– Mar. 1971	4	141	75.9	66	42.4	36	80.6	20	65.0		
Apr.–June 1971	3	77	97.4	46	89.1	11	36.4	22	95.5	44	68.2
July–Nov. 1971	5	92	98.9	112	99.1	84	86.9	31	83.9	77	92.2
Dec. 1971– Mar. 1972	4	13	92.3	27	100.0	116	90.5	4	75.0		
May 1970– Mar. 1972	23	493	89.7	462	85.9	269	84.0	92	82.6	215	80.5

*Trappability (T) is the number of individuals actually caught expressed as a percentage of the number of individuals known to be alive at the time (N), and summed over the periods indicated. December to March is the period of substantial snow cover; April to June is the interval between loss of snow cover and appearance of juveniles in the trappable portion of the population; and July to November is the period of population recruitment.

1970. The population increased in two phases, during the summer and early winter, to a high in January and February 1971 and then declined toward spring. A rapid increase was noted during the summer of 1971, with a peak in September. The population then declined during the autumn. In early winter it increased rapidly to a peak in February 1972 which was over four times the high reached during the winter of 1970–1971. From this point the population declined rapidly toward the spring of 1972. The bimodal nature of the annual cycle of abundance described for *Blarina* is unique in relation to reports in the literature. We do not know whether this is a common occurrence since the second higher peak occurred during midwinter, a time period largely ignored in small-mammal studies, particularly in northern regions. A number of investigators have reported limited variation in population levels (Patric, 1962; Blair, 1948; and Terman, 1966), but data from other studies reflect a great deal of variation from year to year (Barbehenn, 1958; New, 1959; Manville, 1949; Gottschang, 1965; and Buckner, 1966). The maximum density of 5.2 individuals per hectare (2.1/acre) was reached in February 1972. Although this is considerably less than some reported densities (Manville, 1949, and New, 1959), other studies provide density estimates of the same magnitude (Shull, 1907; Blair, 1948; and Buckner, 1966).

Microtus pennsylvanicus. In the study area habitat suitable for *Microtus* is limited to the scattered swamps dominated by grasses, carex, or sphagnum. These habitats are marginal because of their small size and general isolation within the broader forested habitat and because of seasonal flooding. There is a 3.5-ha open grassy area approximately 500 m from the center of site 1 (200 m from the control area) which may be contributory to the presence of *Microtus*. When trapping began in May 1970, the population was low (Fig. 1). Numbers captured gradually increased until August, then declined until November 1970, and again increased gradually to a peak in June 1971. From this point, a gradual decline occurred until no captures were obtained from February to April 1972, the last month reported on here.

One anomaly noted was the increase in population during the winter of 1970–1971 following the 1970 autumn decline. Because no evidence for winter breeding was found, it is assumed that this increase in population was caused by immigration and/or a change in behavioral response to the trapping procedure.

Habitat suitable for *Microtus* amounted to approximately 1.9 ha (4.6 acres). Using this figure rather than the total grid size, we found that maximum density attained (June 1971) was about 5.3 individuals per hectare (2.1/acre). Although this is considerably less than densities reached in prime habitat, it

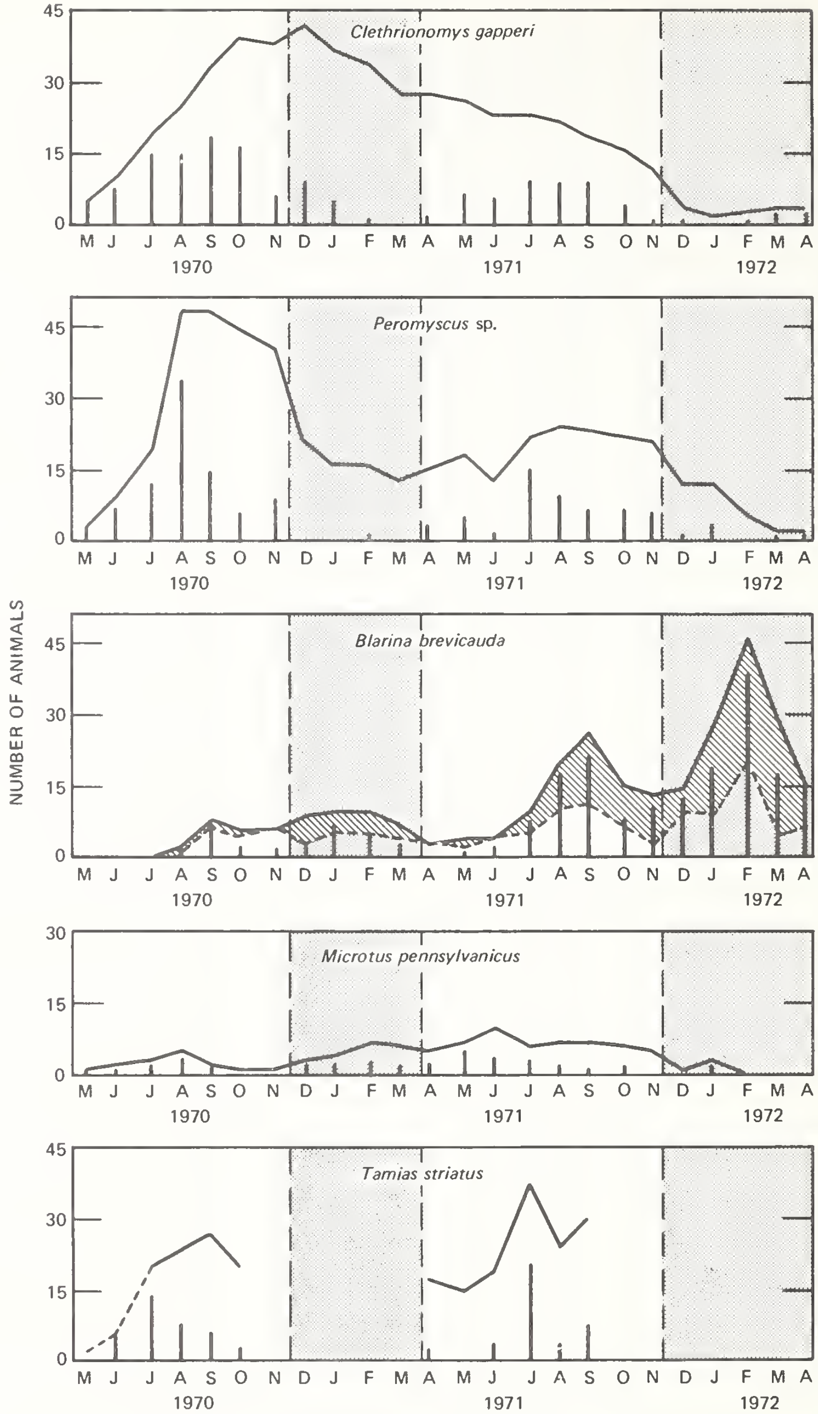


Fig. 1 The minimum number of individuals known to be alive, by species, in site 1 and the control area combined from May 1970 to April 1972. The solid curves (—) represent the minimum number of animals known to be alive. The vertical bars below the curves represent the number of new captures, i.e., animals not previously captured. The shaded area between the solid and dashed curves for *Blarina* represents the number of animals lost to trap mortality. The shaded areas off the time axis show the periods of continuous snow cover. The dashed portion of the curve (----) for *Tamias* indicates a gap in records.

probably approaches the maximum expected for this type of discontinuous habitat. Manville (1949) reported a similar maximum density of 0.89/acre in a northern white cedar swamp.

Tamias striatus. Trapping for *Tamias* initially presented some problems because of escapes from traps. It was not until July 1970 that escapes were eliminated; thus the first two-months' data are not representative (Fig. 1). During the 1970 breeding season, the population peaked in September and declined in October, the last month captures were made before the winter dormant period. The spring population in 1971 was slightly lower than that of the previous autumn (85%). It then rose abruptly to a peak in July which was 40% greater than the peak that occurred in September 1970. After a decline in August, a second, lower peak occurred in September. No captures were made in October 1971, and in the spring of 1972 the population was again lower than that of the previous autumn (77%). Maximum density, which occurred in July, was 4.2 individuals per hectare (1.7/acre). In comparison, Manville (1949) reported a maximum density of 0.72/acre and Burt (1940), 3.62/acre.

Table 3

LENGTH OF THE BREEDING SEASON BY SPECIES FOR THE PERIOD MAY 1970 TO APRIL 1972

Species	Year	Length of breeding season*
Clethrionomys	1970	. . .-Sept.
	1971	Apr.-Sept.
	1972	Apr.-. . .
Peromyscus	1970	. . .-Oct.
	1971	Apr.-Sept.
	1972	Apr.-. . .
Microtus	1970	. . .-Aug.
	1971	Apr.-Sept.
	1972	
Tamias	1970	. . .-Aug.
	1971	Apr.-Sept.
	1972	Mar.-. . .
Blarina	1970†	
	1971	Apr.-Aug. Oct.-Dec.
	1972	Feb.-. . .

*All trapping periods were during the middle of the month; thus April represents mid-April, etc. All species (except possibly *Blarina*) were in breeding condition when trapping was initiated in May 1970. Breeding season was determined from females with medium-to-large nipples and adjusted by the length of the gestation period.

†Data are not available at this time.

Reproduction

Assessment of reproductive condition from autopsies is not possible in a trap and retrap study. The next best procedure is to observe external signs of reproductive activity. Therefore the classification system of Krebs et al. (1969) was used. The most reliable indicators of breeding condition were percent of females with medium-to-large nipples and, secondarily, testes position in males (for all except *Blarina*). Using these indicators and adjusting the initiation of breeding activity derived from percent of adult females with medium-to-large nipples by the length of gestation period, we determined the length of the breeding season (Table 3). Only data for adults (age class defined by body weight) were used. The proportion of adult females with medium-to-large nipples was used as a measure of breeding intensity; Fig. 2 presents this percentage by species for the entire sampling period, May 1970 to April 1972. Also included is the mean percent for the breeding season (sample size is in parenthesis), for all species except *Blarina*.

Clethrionomys gapperi. Breeding in *Clethrionomys* was restricted to the months of April to September (Table 3). This agrees with the reports of Criddle (1932) in southern Manitoba and Coventry (1937) in Ontario. Manville (1949) reported that voles in northern Michigan began breeding in early May. All these reports agree with Evernden and Fuller's (1972) observation from the literature that *Clethrionomys* does not breed in winter, at least in regions with prolonged snow cover.

Peak breeding intensity occurred during June in both 1970 and 1971 (Fig. 2). Intensity was greater during the population decline (1971) than during the increase (1970) phase in that there were more adult females available for breeding and higher percentages of lactating females. Clearly, either the Enterprise vole population experienced increased mortality pressure and declined despite higher breeding intensity or there was a reduction in litter size. At this stage of the analysis, there is no direct evidence to support either of these alternatives. In a New York study, Patric (1962) found that litter size and percent of adult females pregnant were both inversely proportional to population density. He concluded that *Clethrionomys* "reproduced more successfully" during population lows. Perhaps more accurately stated, he found the lowest mean embryo count per gravid female and the lowest percent of adult females pregnant when July indices of population densities were highest. In spite of ambiguities resulting from lack of a definition for such terms as "adult" and "reproductive success" and an apparent lack of consideration of age structure, there is one near-common denominator for comparative purposes: His percent of adult females pregnant is somewhat analagous to percent of adult females with medium-to-large nipples as a measure of breeding intensity. For *Clethrionomys* in the Enterprise Forest, however, a large disparity existed in percent of adult females with medium-to-large nipples in 1970 and 1971 when July densities were essentially equal. Thus data collected to date for Enterprise *Clethrionomys* do not support Patric's findings.

Peromyscus sp. The duration of the breeding season for *Peromyscus* sp. (Table 3) from April to September in 1971 and into October in 1970 agrees with the report of Manville (1949) for *P. maniculatus gracilis.* In a northern Michigan study, Blair (1942) reported that one-third of the mature female *P. maniculatus gracilis* were breeding in the period from September 16 to 22. In southern Michigan the breeding season extends for a longer period of time (Burt, 1940), and in Kansas breeding was recorded from September to March during an exceptionally mild winter (Brown, 1945).

A high breeding intensity was sustained for a longer period of time during 1971 as compared with a single, shorter-lived peak in 1970 (Fig. 2). Although the numbers of adult females captured during both breeding seasons were approximately equal, a higher percentage were lactating during 1971. The data do not support the observation of Burt (1940) of a midsummer lull in breeding intensity in a southern Michigan population of *P. leucopus.* The pattern more closely resembled that for *P. maniculatus gracilis* described by Manville (1949), who reported no lull in intensity.

As was the case for the 1971 population of *Clethrionomys,* recruitment to the 1971 population of *Peromyscus* was poorer than in 1970 despite indications that breeding intensity was greater in 1971. At present we cannot identify the

factors that may have contributed to the apparent reduction in recruitment during the 1971 breeding season.

Blarina brevicauda. A problem was encountered in determining breeding conditions for *Blarina* because of the difficulty of making reliable determinations of sex in all live animals except obviously pregnant or lactating females. Data for females collected from May 1970 to April 1971 were omitted because of the small sample available. Determination of the length of the breeding season was based primarily on dead females obtained from trap mortality between May 1971 and April 1972 (Table 3). During this period of generally high populations, there were only two months, September and January, during which no females with medium or large nipples were caught; this indicates that the species is capable of year-round reproduction. To eliminate any possible biases in sex recognition for live animals, we used only dead adult females to assess breeding intensity (Fig. 2). Intensity was oscillatory in nature and apparently synchronous among females in the population. In May 1971 only one lactating adult female was recorded. However, other records from live females indicate that some were lactating during the period from May to June. None of the nine carcasses subsequently obtained during August and September were lactating. From October to December 1971, 21% of 19 adult females were lactating, but none of the eight dead females captured in January 1972 were lactating. From February to April 1972, 46% of 24 adult females were lactating.

Numerous opinions have been published with respect to length of the breeding season of *Blarina*. Hamilton (1929) found that two litters were produced annually in New York, one in the spring (with sexual activity commencing early in February) and another in late summer. Manville (1949) reported that two litters are raised during a season in northern Michigan; the first appears in May or June and the second in September after a midsummer resting period in which breeding does not occur. Blus (1971) reported that litters were born during every month of the year in a captive colony. In a New York study, Dapson (1968) reported that most reproductive activity occurred in the spring but that scattered records of breeding were found during all seasons, Christian (1969), in a Pennsylvania winter study, found that the breeding season started in early January and was well advanced by mid-February.

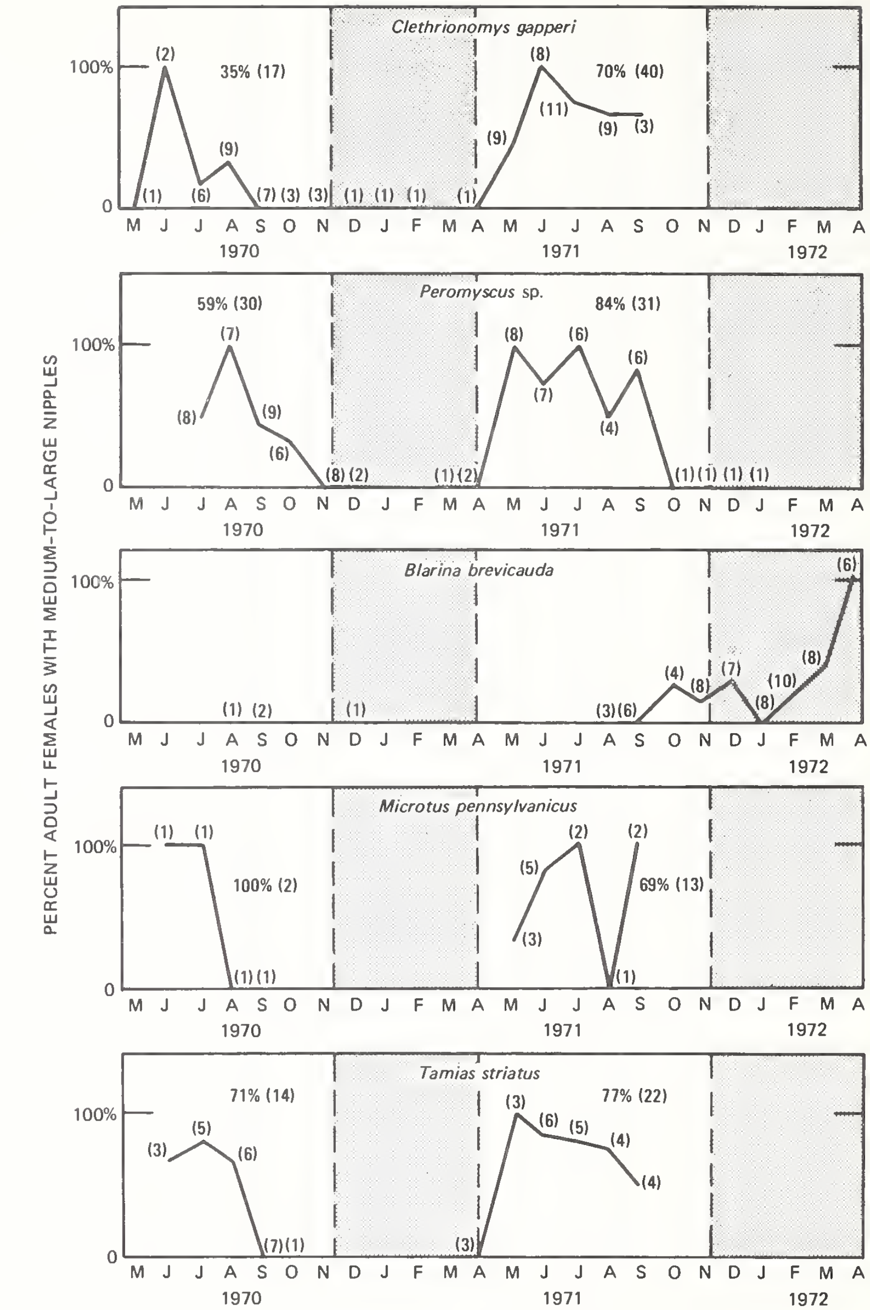


Fig. 2 Percent of adult females with medium-to-large nipples, by species, in site 1 and the control area from May 1970 to April 1972. The number in parentheses beside each point is the sample size. The mean percent for the breeding season (with sample size in parenthesis) is given at the end of the curve for each year for all species except *Blarina*. To eliminate possible biases in sex recognition for live *Blarina*, we used only data from dead adult females. The shaded areas off the time axis show the periods of continuous snow cover.

The Enterprise data confirm the field observations of Dapson (1968) and Christian (1969) of a winter breeding potential for *Blarina*. Although further data collection will help clarify the situation further, we can draw some conclusions: (1) Breeding can occur during almost every month of the year. (2) There is an apparent synchrony among females in breeding effort. (3) Under certain unknown conditions, periods of peak breeding intensity may follow one another in succession after an intermittent period of as little as a month. (4)

It is unknown whether breeding normally occurs in a particular season or whether other factors control sexual maturation so that breeding occurs irrespective of season, e.g., in years when populations reach higher than usual densities.

The net result of the observed peak periods of breeding activity was a subsequent rise and fall in population commensurate with the duration and intensity of the preceding period of breeding activity. Thus the bimodal nature of the population curve described for *Blarina* was a result of timing of breeding activity. As such, it may be temporally and spatially unique to this study and not open to generalizations concerning other populations. Although statements of other investigators referring to two periods of breeding activity support the case for a bimodal annual cycle of abundance, these studies did not include an enumeration on a year-round basis. Thus we do not know if the two periods of breeding activity mentioned were eventually expressed in the population curve as two peaks of abundance.

Microtus pennsylvanicus. The breeding season for *Microtus* was from April to September in 1971 (Table 3) but apparently extended only to August in 1970 (this may be a manifestation of the low number of captures during this period, however). That breeding occurred from April to September is consistent with the report of Manville (1949) in northern Michigan; however, it is well known that at times *Microtus* may breed year-round. Too few adult females were captured during 1970 to make any comparison of breeding intensity between years except in terms of absolute numbers. There were more lactating females during the 1971 season (Fig. 2). This was subsequently reflected in the higher population observed during that summer.

Tamias striatus. The length of the breeding season for *Tamias* is from late March or early April to late August or early September (Table 3). This agrees with data reported by others. Manville (1949) reported that breeding began in April and recorded a lactating female on August 26 in northern Michigan. Burt (1940) reported that breeding began April 1 and that a second period of breeding may occur in late July or early August in southern Michigan. Yerger (1955) reported that females were in heat from March 17 to April 7 in central New York. Smith and Smith (1972) also reported that breeding was initiated in March to April and that lactation persisted as late as September or early October in the eastern half of Canada. All these investigators observed that two litters may be produced during the breeding season. The two influxes of juvenile animals noted in the Enterprise Forest during the 1971 season, in July and in September (Fig. 3), support these data. Maximum numbers of individuals were noted in July 1971 because of the appearance of juveniles in the trappable portion of the population. Data for 1970 are incomplete because of escapes from the traps, but it is probable that the 1970 and 1971 breeding seasons were similar in intensity both in absolute numbers of adult females available for breeding and in percent lactating (Fig. 2). Data for the 1971 breeding season indicate a decline in breeding intensity toward the latter part of the season. If this is the general case, we would expect populations to peak during the early summer emergence of juveniles rather than during the late-summer—early-autumn emergence as was indicated by the incomplete data for 1970.

Body Weight

One method used to characterize populations was to describe the body-weight distribution over time. In addition to the weight distribution, we can arrive at an indirect subjective estimate of the relative proportion of juveniles, subadults, and adults (age defined by body weight). Figure 3 shows the body-weight distribution by species from May 1970 to April 1972. Figure 4 shows the body-weight history of selected individual males for which long-term records were available. Except for *Blarina*, only data

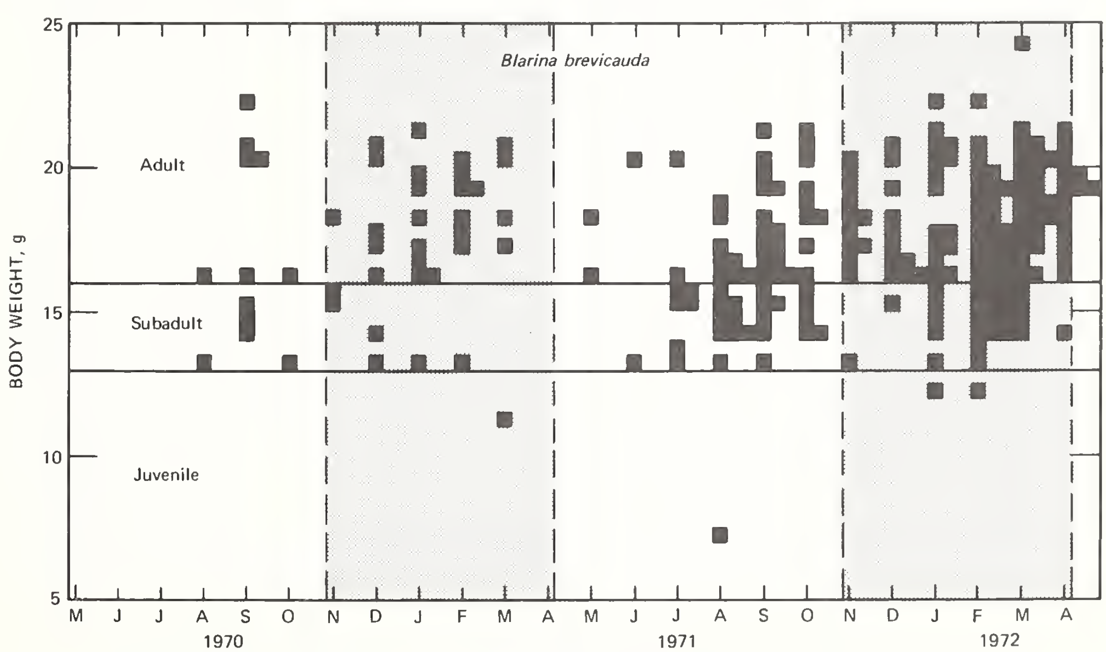
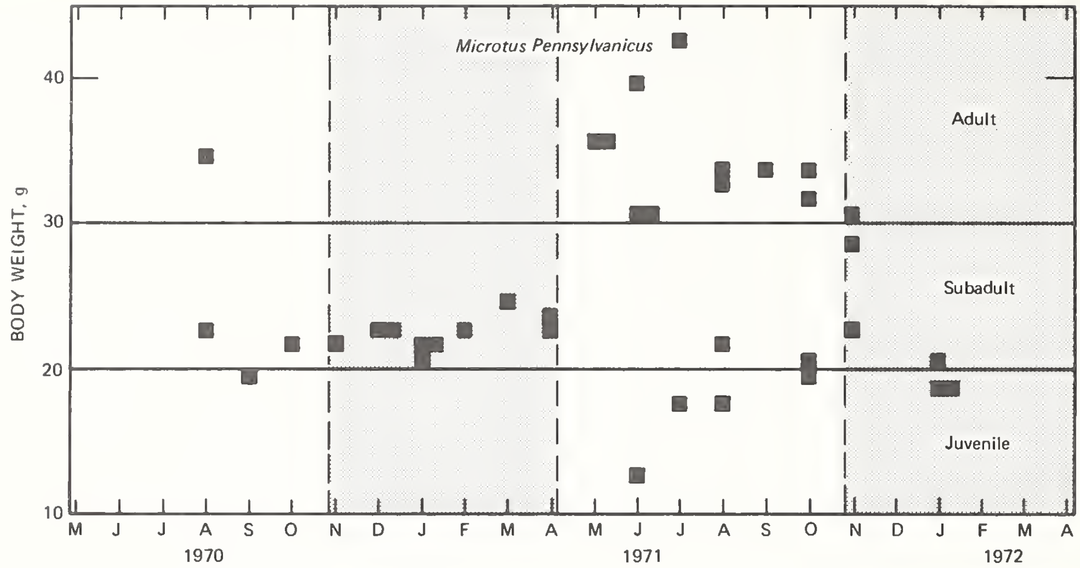


Fig. 3 Body-weight distribution, by species, of individuals caught in site 1 and the control area from May 1970 to April 1972. Only data for males are shown (except for *Blarina* where data for the sexes are combined). The shaded area off the time axis represents the period of continuous snow cover. The weight limits used to distinguish age class are delineated in the figure.



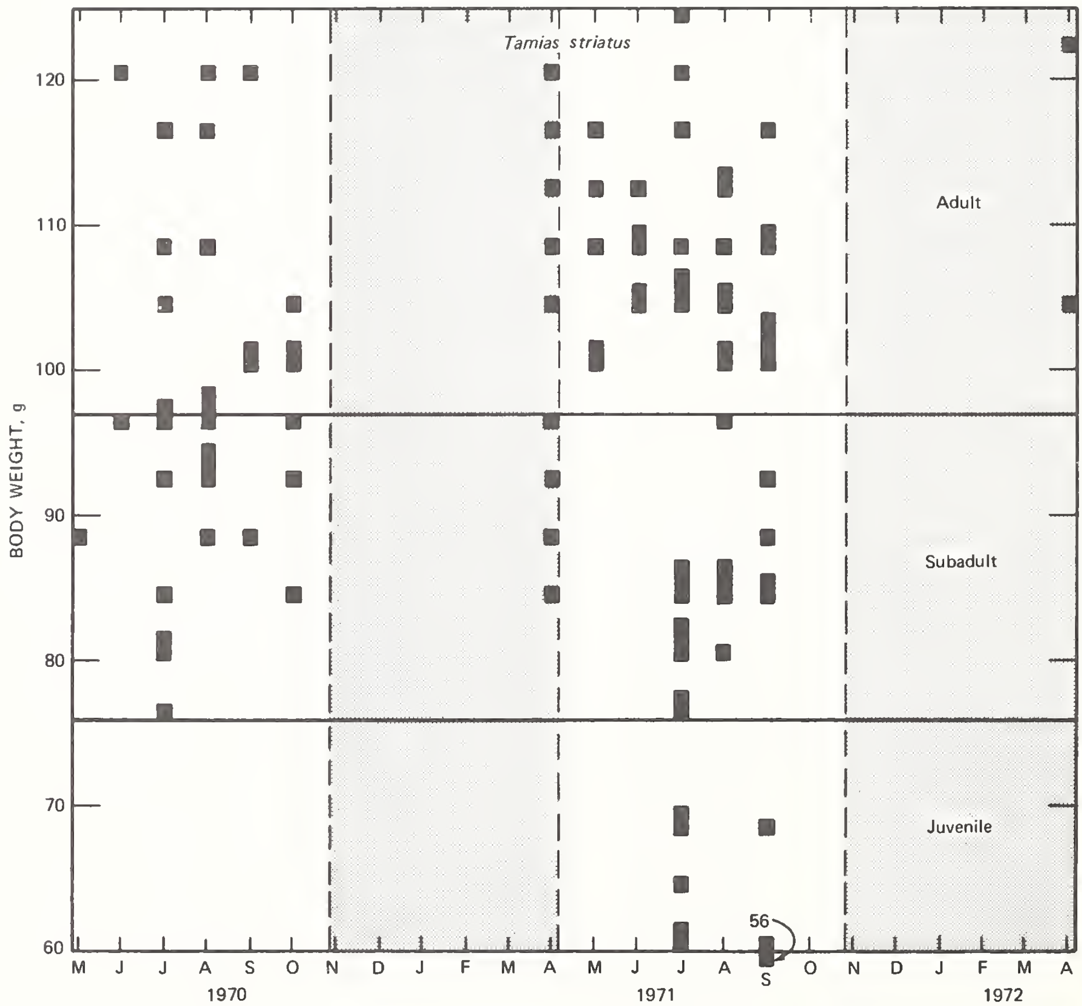
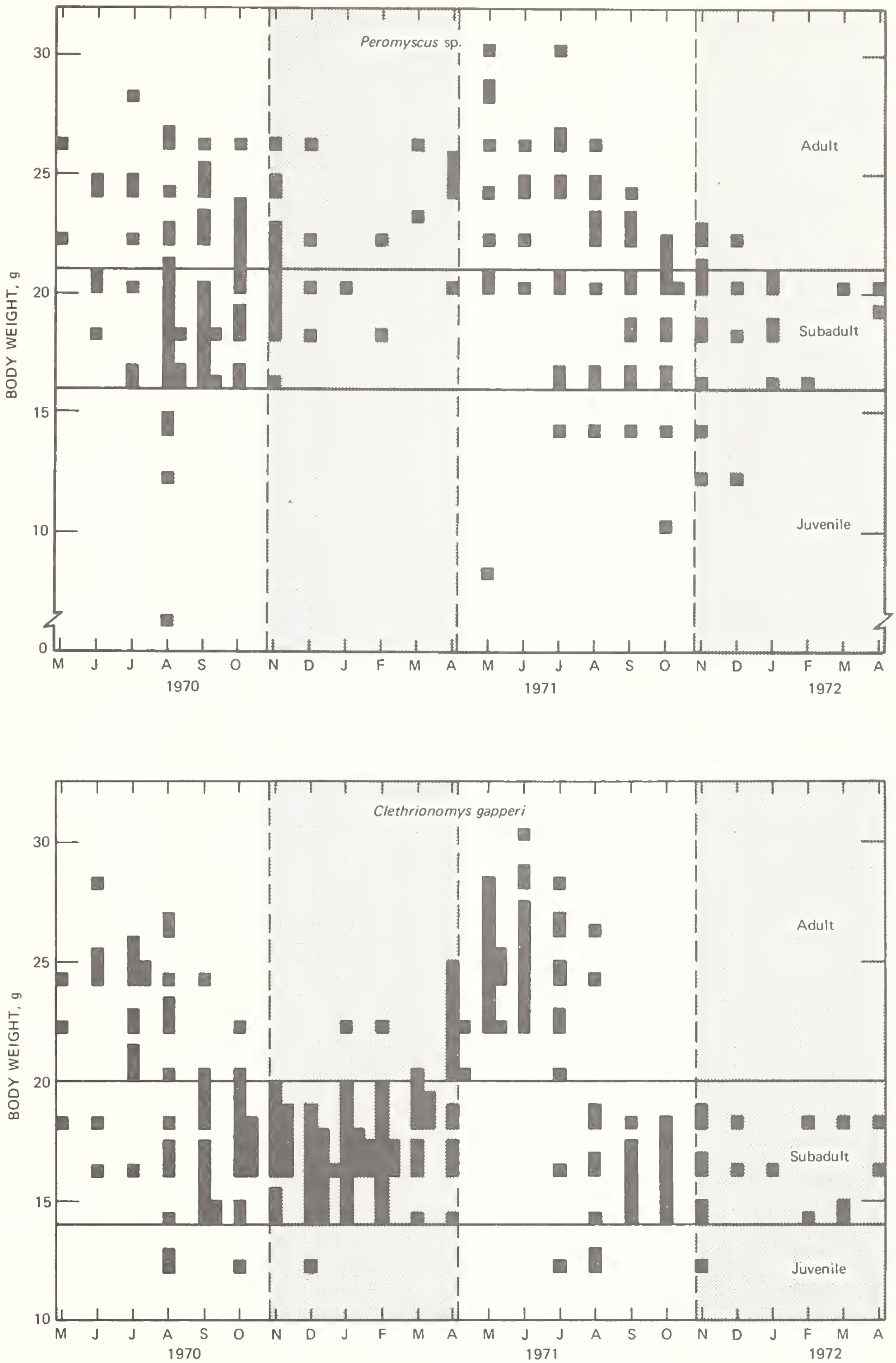


Fig. 3 (Continued)



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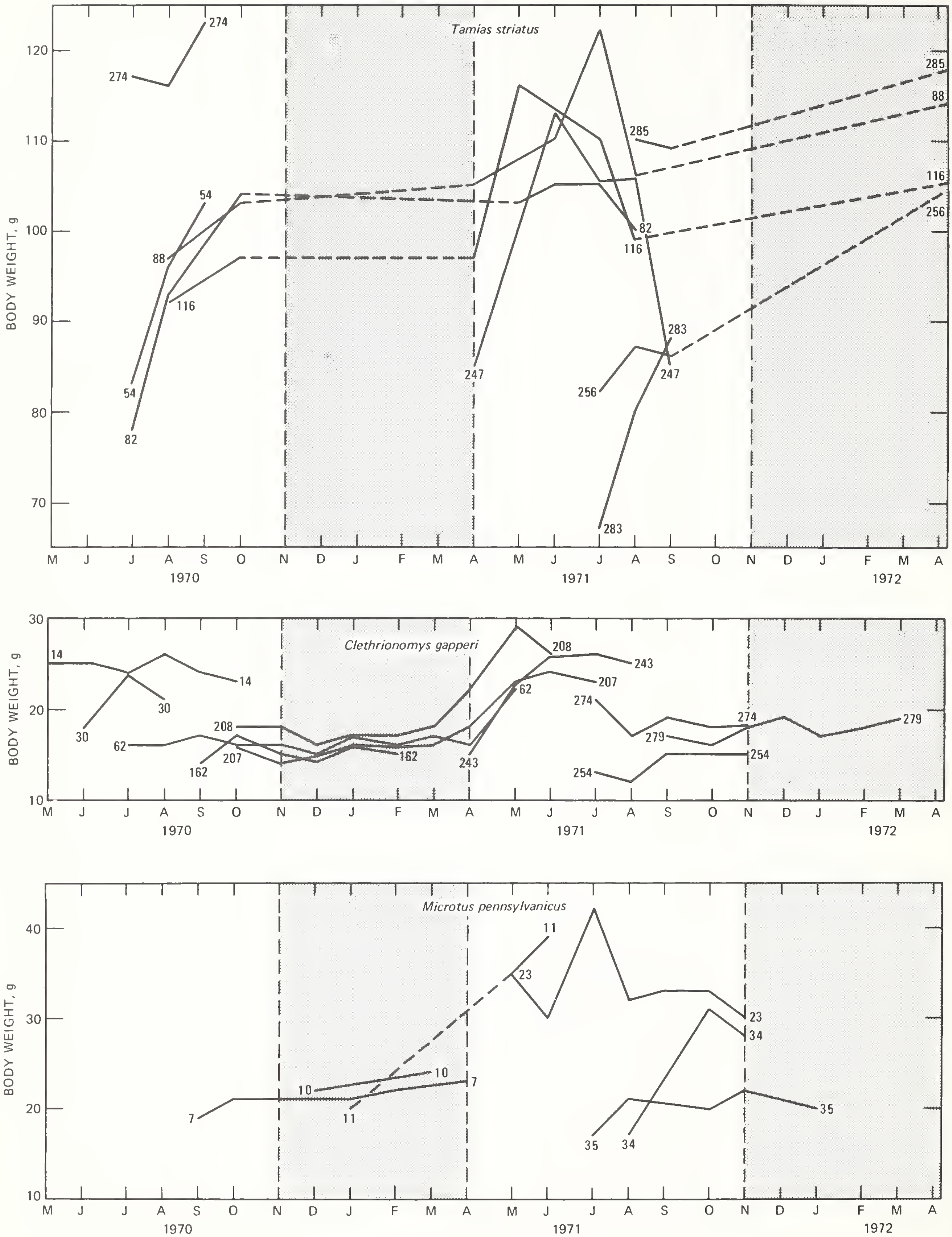

Fig. 4 See facing page for legend.

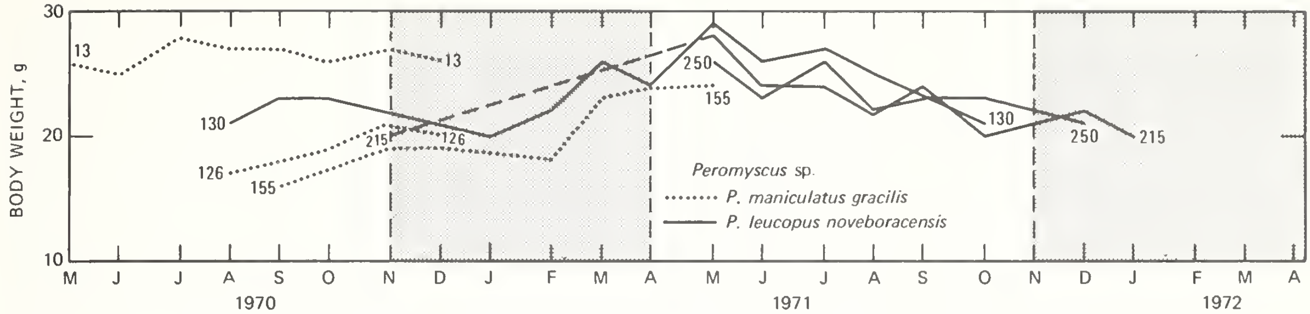

Fig. 4 Body-weight history of selected individual males for which long-term records were available from May 1970 to April 1972. The number given to the individual animal is shown on the curve for each animal. (Insufficient recaptures of *Blarina* precluded construction of individual weight-history curves.) The stippled area off the time axis represents the period of continuous snow cover. The dashed portions of the curves (---) indicate gaps in records.

for males are shown; data for females were similar with the exception that their weights were higher during pregnancy.

Clethrionomys gapperi. Male voles of adult size (>19 g) were found primarily from April to August (Fig. 3). Proportionately the adult size class dominated the distribution from April to July. Numbers of adult-sized voles were larger during the decline than during the increase phase. Despite the larger number of adult-sized voles during the 1971 decrease phase, fewer animals of subadult size were present during the fall and winter of 1971–1972 than during the preceding year of increase. The largest individuals were found during the decline.

Young of the year, first captured during the late summer and early autumn, did not attain a body weight of 20 g until the next spring (Fig. 4). In general, their weight reached an autumn peak (approximately 17 g) and then declined slightly to a temporary low in early winter (approximately 16 g). Weight then remained fairly stable until early spring, when rapid gains brought them to reproductively active adult size (approximately 25 g) by June or July. Records for a few individuals indicate that there is a subsequent decline in weight in the autumn. The situation with respect to individuals born early in the breeding season is unclear because of uncertainties related to age determinations on the basis of weight. However, one individual's records indicated that it had reached near-adult size and was reproductively active during the season of its birth.

Little information is available concerning winter body weights of *Clethrionomys,* and what is available was derived from snap-trap samples. Mean body weight of a population at a given point in time is difficult to interpret unless the age structure of the sample is known. For winter population samples of *Clethrionomys,* this difficulty is of less significance because there is little variation in winter body weights since at this time voles are sexually inactive and the population is composed primarily of animals less than a year old. Fuller, Stebbins, and Dyke (1969), reporting on winter mean body weights for *C. rutilus* and *C. gapperi* from the Northwest Territories, showed that *C. rutilus* in this area had a tendency to lose weight in early winter and regain it in late winter. This winter weight loss was not indicated in *C. gapperi,* but they reported that mean weight stabilized at approximately 16 g. Although there was a midwinter weight loss for *C. gapperi* in the Enterprise Forest, the Enterprise live-trap data generally agree with the data of Fuller et al. Reporting on late-winter body weights of *C. gapperi* from Alberta, Evernden and Fuller (1972) showed that weight gain in late winter and early spring was associated with sexual maturation. Again, Enterprise voles displayed the same gains, similar in time and magnitude. We should note, however, that at no time did the Enterprise voles reach a winter weight of less than 12 g, in contrast to the weight of about 10 g reported by Evernden and Fuller during February.

Peromyscus sp. Adult male individuals of *Peromyscus* sp. (>21 g) were found in almost every month, but they were more prevalent from April to November (Fig. 3). Proportionately the adult size class dominated the distribution from March to July. Although the population peak of 1971 was only about half that of 1970, numbers of adult-sized animals during the months of May and June 1971 were almost twice those of the same period during 1970. Also the largest individuals were captured during 1971.

The literature is almost void of reports of winter weights of *Peromyscus.* This is probably because of the lack of winter small-mammal studies in northern regions and of the low trappability for this species during winter. Fuller et al. (1969) provided mean winter weights of *P. maniculatus* from the Northwest Territories. On the basis of snap-trap samples, they reported a midwinter weight loss. The winter weights of *Peromyscus* in the Enterprise Forest essentially followed the same pattern. Weight histories of three individuals of each species are shown in Fig. 4. In general, weight histories were similar to *Clethrionomys;* young of the year attained larger autumn and overwintering weights, but the pattern remained the same. Growth continued until an autumn apex was reached, then there was a slight weight loss to a temporary low in winter. Rapid gains then occurred in early spring until the animals reached full adult size. The pattern for adults appeared to be associated with breeding activity, i.e., they were heavier during the reproductively active summer months than during the inactive winter months. As was the case for *Clethrionomys,* midwinter weights of *Peromyscus* in the Enterprise Forest did not decrease to the lower weights reported by Fuller et al. (1969).

Blarina brevicauda. There were no seasonal aspects to the occurrence of adult-sized animals (>15 g) in the weight distribution for *Blarina.* Breeding occurred year-round (Fig. 3), and all size classes were represented at any given

month of the year. There were no obvious differences in maximum size attained in relation to population density.

Records were inadequate to construct individual weight curves. High trap mortality was no doubt responsible for the fact that three trapping periods (3 months) was the maximum record for any individual. In most cases the records were of dubious value in that the last capture record usually involved mortality in the trap and attendant starvation, which would tend to reduce the last weight recorded and perhaps the others depending on the length of time the animal spent in the trap. Nevertheless, weight gains were recorded during all months of the year. It is unknown whether the magnitude of the gain varied with respect to season.

Microtus pennsylvanicus. In general, adult-sized males of *Microtus* (>29 g) were found from May to September (Fig. 3). Captures were insufficient to make any annual comparisons. It can be seen, however, that subadult animals (20 to 29 g) dominated the population during the winter months and that juveniles appeared in the population as early as mid-June, e.g., the 13-g animal captured in June 1971.

Comparable weight information for *M. pennsylvanicus* was provided in an Indiana study (Krebs et al., 1969). Individual weight curves shown by Krebs and coworkers indicate that a cessation of growth for young of the year during the winter is not necessarily the general case for *Microtus* in Indiana. They stated: "Growth is clearly associated with breeding seasons, and winter breeding during the increase phase of the cycle is closely linked with good winter growth." Data for meadow voles at Enterprise demonstrated the same pattern we observed for *Clethrionomys* and *Peromyscus:* That is, individuals born in late summer temporarily quit growing in the fall and winter until spring (Figs. 3 and 4). In relation to the conclusions of Krebs et al. we must note that breeding did not occur during the winter at Enterprise as it did in Indiana.

Tamias striatus. Owing to the relatively longer life span of *Tamias,* adult-sized animals were found during every month that captures were made (Fig. 3). Since young of the year are not trappable until after mid-June and thus small animals trapped early in the year must be adults, it can be seen that early spring weights of adults may be as low as 84 g, e.g., in April 1971. The only obvious difference in the weight distribution between 1970 and 1971 was when a second influx of juvenile animals occurred in September 1971.

The longevity of *Tamias* permits a view of weight history over a longer time period and thus gives a better view of growth and weight variation with respect to season. In another respect, however, there are voids in the data during the dormant period. In general, the following conclusions were drawn (Fig. 4): (1) Body weights of spring-born individuals approximated those of adults by September or October, whereas fall body weights of midsummer-born individuals were less than adult weights. (2) Adult weights vary considerably with respect to season. Figure 4 and other data not shown indicate a general increase in adult weight in spring and a decrease in summer. This is most probably a reflection of reproductive condition. (3) Although the last autumn and first spring capture weights are not equivalent to pre- and post-dormant period weights, animals with the shortest time interval between autumn and spring captures indicate no obvious weight change associated with the dormant period (e.g., Nos. 82, 99, and 116). This implies that the gain in weight shown by spring-born individuals during their second summer accrued after emergence from hibernation. The situation with respect to those born in midsummer is unknown since in all cases the interval between autumn and spring captures was too long to determine whether the gains accrued during the dormant period or after emergence in the spring. Smith and Smith (1972) believed midsummer-born young reached adult weights before spring emergence. However, this conclusion was based on an absence of animals weighing less than adult size in spring collections.

SUMMARY

A live-trap study of small-mammal populations and their response to gamma radiation is in progress in the Enterprise Radiation Forest near Rhinelander, Wisconsin. Trapping in northern forest communities has been conducted on a monthly basis since May 1970 on two grids totaling 8.9 ha in size. Data gathered from the two grids before radiation treatment (through April 1972) were combined to present information concerning the trappability, populations, reproduction, and body weight of the most prominent species. Species covered are the red-backed vole (*Clethrionomys gapperi*), the short-tailed shrew (*Blarina brevicauda*), the eastern chipmunk (*Tamias striatus*), the meadow vole (*Microtus pennsylvanicus*), the woodland deer mouse (*Peromyscus maniculatus gracilis*), and the white-footed mouse (*P. leucopus*). Data for the last two species were lumped together as *Peromyscus* sp.

Trappability, the number captured expressed as a percent of those known to be alive, was determined on a seasonal basis for each species. These figures indicate that *Clethrionomys* and *Peromyscus* are more readily captured than *Microtus* or *Tamias.* For *Blarina* trappability was directly proportional to population density.

The *Clethrionomys* population increased (1970) and decreased (1971) over a period of two years. In contrast, *Peromyscus* underwent an annual cycle of increase and decrease, the peak population of 1971 being only half that of 1970. The annual cycle of abundance for *Blarina* was bimodal, with the highest peak occurring during January or February. The peak population during the winter of 1971–1972 was four times that of the previous winter. For *Microtus* marginal habitat contributed to a low number of captures. From a high in August 1970, numbers declined in the autumn until winter, when captures irregularly increased to a peak in June 1971. The population then declined to extinction by February 1972. *Tamias* underwent an annual cycle of increase and decrease during the breeding season. Spring populations were 85 and 77% of the population entering the dormant period in the spring of 1971 and 1972, respectively. The highest density attained for each species during the study were: *Clethrionomys,* 4.7 individuals per hectare; *Peromyscus,* 5.4/ha; *Blarina,* 5.2/ha; *Microtus,* 5.3/ha; and *Tamias,* 4.2/ha.

Except for some annual variation, the breeding season for all species except *Blarina* extended from April to September. Year-round breeding was noted for *Blarina.* Although breeding is apparently synchronous, it is unknown whether seasonality or other factors contributed to

the observed periods of breeding for *Blarina*. Breeding intensity was greater in 1971 than in 1970 for *Clethrionomys, Peromyscus,* and possibly *Microtus*. No difference in breeding intensity was detectable for *Tamias* between the two years. For *Blarina* intensity was oscillatory in nature, with each peak being greater than the last.

Data obtained from body-weight distributions and individual weight histories indicate that for species reproductively quiescent during the winter (in northern regions at least), there is an interruption of growth for young of the year during the winter. In the spring the animals gain weight rapidly until they reach reproductively active adult size. For adults there appears to be a basal weight to which an individual returns after the weight gains expressed during the breeding season. Thus, in addition to such factors as nutrition, genetic potential, etc., body weight may also be influenced by reproductive state, age (especially available time to grow prior to winter), and season of the year.

Future data collection and analysis will permit expansion of the interpretations and conclusions presented here.

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DISCLAIMER

The use of trade, firm, or corporation names in this paper is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the U. S. Department of Agriculture of any product or service to the exclusion of others which may be suitable.

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Predicted Effects of Chronic Gamma Irradiation on Northern Forest Communities*

13

J. ZAVITKOVSKI, T. D. RUDOLPH, and E. O. BAUER†

Institute of Forest Genetics, North Central Forest Experiment Station, Forest Service, U. S. Department of Agriculture, Rhinelander, Wisconsin

ABSTRACT

A prediction of the effects of gamma radiation (growing-season exposure) on natural northern forest communities has been developed based on vegetation survey, determination of interphase chromosome volumes (ICV) of the most important plant species, and reported relationships between ICV and radiosensitivity. The ICV's of angiosperm tree, shrub, and ground-vegetation species ranged from about 1.5 to 7.3 μ^3, *and those of gymnosperm trees from 30.2 to 52.0* μ^3. *Lichens and bryophytes are common and because of their high radioresistance should survive in the innermost zone. A* Carex *zone with some Lycopodiaceae should develop around this innermost zone; this should be followed by a zone dominated by* Corylus cornuta *and several species of Ericaceae. The transition between the third and fourth zone may be very diverse, with* Corylus *and* Amelanchier, *some Polypodiaceae, and perhaps some resistant tree genera such as* Tilia, Fraxinus, *and* Prunus. *Sprouts from roots of killed* Populus tremuloides *trees also may develop and survive here. Beyond this, a zone dominated by* Betula, Populus, *and* Acer *in its inner part with some* Quercus borealis *at the outer edge should become evident but may not be too different from the pretreatment forest because only gymnosperms will be selectively removed. Living gymnosperms will delineate the outermost zone of essentially unchanged northern forests.*

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Effects of gamma radiation on vegetation can be predicted within broad limits from established relationships between some nuclear parameters [e.g., nuclear volume (NV), interphase chromosome volume (ICV), and DNA content] and radiosensitivity of plants composing the community (Sparrow and Miksche, 1961; Sparrow and Woodwell, 1963; Sparrow, 1965; Miksche and Rudolph, 1967; Sparrow et al., 1970). However, these relationships are usually determined under controlled conditions in which effects of the environment and other factors are minimized. Thus their application to a natural plant community should consider the modifying effects of environmental factors and make proper adjustments for them (Sparrow and Woodwell, 1963; Woodwell and Oosting, 1965).

Environmental stresses modify radiation effects on plants by reducing both the exposure at which significant plant changes occur and the overall range of radiosensitivity determined for plants under controlled conditions (Woodwell, 1963; Woodwell and Sparrow, 1963). Among the plant factors that tend to modify the established relationships, the plant life form, reproductive habit, season of irradiation, and ecological tolerance are important.

Results of several studies (Woodwell and Oosting, 1965; Brayton and Woodwell, 1966; Woodwell and Gannutz, 1967; Woodwell and Rebuck, 1967) indicate that herbaceous and shrub species with a spreading form of growth are in general more radioresistant than the upright forms. Within the tree stratum, however, this generalization may not apply, as larger pine and oak trees were generally more radioresistant than small trees; this can perhaps be explained by a greater vigor or larger number of buds on the larger individuals (Woodwell and Rebuck, 1967; McCormick, 1969). Studies by Wagner (1966) have shown that perennial plants with shielded perennating buds and vigorous asexual reproduction are relatively radioresistant. Other studies have indicated that plants adapted to extreme habitats such as old fields or granite rock outcrops, and plants typical of early successional stages are, in general, also radioresistant (McCormick and Platt, 1962; McCormick, 1963; Woodwell and Oosting, 1965; Miller, 1968; Woodwell, 1970). Seasonal variations in plant radiosensitivity have been reported for herbaceous species and longleaf pine (*Pinus palustris*) by Miller (1968), and for eastern white pine (*Pinus strobus*) by Sparrow et al. (1970). In both studies an equivalent growing-season exposure caused more damage than dormant-season exposure.

Selection of an appropriate end point for evaluating radiation effects on plants is very important and may become a problem in predicting radiation damage in natural plant communities. Inhibition of vegetative growth or reproductive capacity and death have been used, singly or in combination, in radiation studies. Although reproductive stages are almost always more radiosensitive than vegetative stages (Sparrow and Woodwell 1962, 1963), relative radiosensitivity of plant species measured simultaneously by these two end points may differ. For example, Mergen and Stairs (1970) report that,

although pitch pine (*Pinus rigida*) is more radiosensitive in terms of vegetative growth than oaks, sensitivity measured by germination of seed collected from irradiated trees along a radiation gradient was similar for both species. Differences in observed radiosensitivity of tree seeds and seedlings, depending on the end point used, have also been demonstrated by Rudolph and Miksche (1970) and Rudolph (1971). Even if death is used as the end point, questions arise: Does it refer to the aboveground portions of a plant or the entire plant? Should sprouts of apparently "killed" plants, such as may occur in *Populus*, be considered as new plants or "revived" original plants?

In this paper we attempt to predict effects of chronic gamma irradiation during one growing season on a natural northern forest ecosystem. Our prediction is based on reported relationships between some nuclear variables and radiosensitivity, results of similar irradiation studies in other forest ecosystems, and our own determinations. This prediction is still only an approximation, despite the fact that more information is available today than ten years ago when Sparrow and Woodwell (1962, 1963) predicted the radiation effects on the Brookhaven oak–pine forest ecosystem. The main reason for the uncertainty is the much greater complexity of northern forest ecosystems as compared with that at Brookhaven. The ecosystems in our experimental area are composed of more than 200 higher plant species forming heterogenous communities in areas with uneven topography and with evidence of past disturbances.

A semiportable 10,000-Ci ^{137}Cs source will be used in this study. This source, which was used in a radioecological study at El Verde, Puerto Rico, is described in detail by Odum and Drewry (1970).

DESCRIPTION OF THE EXPERIMENTAL AREA AND ITS VEGETATION

The area selected for the growing-season irradiation is within a fenced 1440-acre experimental tract in the town of Enterprise, near Rhinelander in north-central Wisconsin. Three distinct forest types—aspen, birch, and northern hardwood—account for more than 80% of the 7.06 ha encompassed within a 150-m radius around the gamma source. Bogs, with their typical vegetation of tamarack (*Larix laricina*), black spruce (*Picea mariana*), yellow birch (*Betula alleghaniensis*), speckled alder (*Alnus rugosa*), bog laurel (*Kalmia polifolia*), Labrador tea (*Ledum groenlandicum*), sedges, and mosses, account for about 17% of the remaining area and old logging roads for about 2%. A vegetation survey of the area revealed the presence of 28 tree species (9 gymnosperms and 19 angiosperms), 17 shrub species, and about 140 herbaceous species.

Table 1

RELATIVE DENSITIES OF TREE SPECIES IN THE ENTERPRISE RADIATION FOREST*

Species	Relative density, %
Populus tremuloides	31.8
Acer rubrum	24.3
Betula papyrifera	8.2
Acer saccharum	7.8
Fraxinus nigra	7.5
Prunus serotina	3.1
Ostrya virginiana	3.0
Tilia americana	2.8
Salix sp.	2.3
Amelanchier sp.	1.7
Betula alleghaniensis	1.5
Quercus rubra	1.0
Abies balsamea	0.8
15 additional species	<1.0

*Relative densities are based on a complete tally of 1672 living trees present within a 50-m radius from the source (or in an area of 0.785 ha). Only trees with a dbh larger than 2.5 cm are included.

Results of a complete tally of trees larger than 2.5 cm in diameter at breast height (dbh) growing within a 50-m radius of the gamma source (Table 1) showed that quaking aspen (*Populus tremuloides*) and red maple (*Acer rubrum*) together accounted for more than half of the total trees, followed by paper birch (*Betula papyrifera*), sugar maple (*Acer saccharum*), and black ash (*Fraxinus nigra*), each with more than 7.5% of the total. The most common conifer, balsam fir (*Abies balsamea*), made up only 0.8% of the total. Beaked hazel (*Corylus cornuta*) was the most important shrub, with relative densities of more than 85 and 50% for tall and low shrubs, respectively (Table 2). Only two other low shrub species, blackberry (*Rubus allegheniensis*) and velvet-leaf blueberry (*Vaccinium myrtilloides*), reached relative densities of over 10%. No tall shrub species other than beaked hazel even approached that figure. Three herbaceous species, *Carex pensylvanica*, *Aster macrophyllus*, and *Oryzopsis asperifolia*, had frequencies higher than 50% (Table 3), seven additional species higher than 25%, and 15 other species higher than 10%. Among woody seedlings, which were arbitrarily included in the ground-vegetation layer if their height was less than 30 cm, three reached frequencies higher than 25% and ten others higher than 10% (Table 4). No quantitative data are available for the lower plants, but both mosses and lichens were abundant throughout the area.

Table 2

RELATIVE DENSITIES OF TALL AND LOW SHRUB SPECIES IN THE ENTERPRISE RADIATION FOREST*

Species	Tall shrubs,† %	Low shrubs,‡ %
Corylus cornuta	85.8	50.5
Rubus allegheniensis	1.0	20.7
Vaccinium myrtilloides		11.8
Ilex verticillata	3.5	1.6
Amelanchier sp.	1.7	2.8
Prunus serotina	1.0	1.6
Fraxinus nigra	<1.0	1.8
Populus tremuloides	1.1	1.7
Salix sp.	<1.0	1.5
Acer rubrum	<1.0	1.4
Diervilla lonicera		1.2
12 additional species	<1.0	<1.0

*Based on a sample of shrub vegetation within a 50-m radius from the source. An estimated total of 13,000 tall and 22,000 low shrubs are present within this area.

†All woody vegetation from 1 m in height to 2.5 cm in dbh.

‡All woody vegetation 0.3 to 1 m in height.

Most trees ranged in age from about 35 to 45 years, with occasional individuals over 80 and aspen thickets less than 20 years old. The average height of the tree canopy was about 18 m, with the tallest trees being about 24 m. The 1969 survey of the inner 50-m-radius area (about 0.785 ha) revealed the presence of 1672 living trees (corresponding to 2129 trees/ha) with a dbh over 2.5 cm. These trees were of both seed and vegetative origin, with a high proportion of forks and clusters arising from stump sprouts. The origin of shrubs and ground vegetation was mostly vegetative. Preliminary observations indicated that, except for some of the tree species, seed production of all ecosystem components was low.

The aboveground standing-crop dry weight (DW) of trees was estimated from

Table 3

FREQUENCIES OF HERBACEOUS SPECIES IN THE ENTERPRISE RADIATION FOREST*

Species	Frequency, %
Carex pensylvanica	87.3
Aster macrophyllus	70.7
Oryzopsis asperifolia	64.7
Maianthemum canadense	42.3
Aralia nudicaulis	42.0
Cornus canadensis	39.7
Viola pallens	39.0
Pteridium aquillinum	37.0
Gaultheria procumbens	35.3
Lycopodium obscurum	32.3
Trientalis borealis	22.3
Carex sp. (*except C. pensylvanica*)	21.3
Waldsteinia fragarioides	20.7
Pyrola virens	19.7
Fragaria virginiana	18.3
Mitchella repens	15.3
Clintonia borealis	14.3
Brachyelytrum erectum	13.7
Galium triflorum	13.3
Hieracium sp.	13.3
Pyrola rotundifolia	12.7
Streptopus roseus	11.3
Luzula acuminata	11.0
Aster umbellatus	10.3
Lycopodium clavatum	10.0

*Frequencies (percent of plots in which the species is present) are based on presence in 332 1-m² plots.

Table 4

FREQUENCIES OF WOODY SEEDLINGS IN THE ENTERPRISE RADIATION FOREST*

Species	Frequency, %
Acer rubrum	40.3
Corylus cornuta	33.0
Diervilla lonicera	30.0
Fraxinus americana	23.3
Acer saccharum	20.7
Rubus allegheniensis	19.8
Prunus serotina	19.3
Betula papyrifera	18.7
Abies balsamea	16.3
Amelanchier sp.	15.3
Vaccinium myrtilloides	13.0
Rubus pubescens	11.0
Quercus rubra	10.3
Populus tremuloides	7.7
Fraxinus nigra	5.7
Rubus strigosus	5.3

*Frequencies (percent of plots in which the species is present) are based on 332 1-m² plots. Included are species with a frequency of at least 5%. Woody seedlings are individuals less than 30 cm in height.

the average canopy height (Zavitkovski and Stevens, 1971) at about 150 tonnes/ha with an estimated additional 40 tonnes/ha below the ground. Shrubs and ground vegetation add little DW, probably not surpassing 10 tonnes/ha, thus bringing the total vegetation DW to about 200 tonnes/ha.

METHODS USED FOR PREDICTING RADIATION DAMAGE

Basically the predictions build on reported relationships between nuclear characteristics of plants and their radiosensitivity (Sparrow, 1965; Sparrow and Sparrow, 1965; Miksche and Rudolph, 1967; Sparrow et al., 1970), as well as on reported results from irradiation studies in other natural forest ecosystems (Daniel, 1963; Woodwell and Sparrow, 1963; Woodwell and Oosting, 1965; Brayton and Woodwell, 1966; Monk, 1966; Woodwell and Rebuck, 1967; McCormick, 1969; Woodwell, 1970). Our own work included a vegetation survey, which is briefly described in the previous section, and measurements of nuclear volumes of the important woody and herbaceous species growing in the area. The plant material was collected in late summer and consisted of three terminal buds each from two individuals of each woody species and at least three perennating buds from herbaceous species. After processing (Sparrow et al., 1965), NV's were calculated from measurements of eight nuclei of each bud on photomicrographs, and ICV's were obtained by dividing NV's by somatic chromosome numbers (Table 5).

The main end point used in this prediction was the "lethal" dose expressed in roentgens per day for a chronic (one growing-season) irradiation. Exposures that produce severe growth inhibition and LD_{50}'s were also predicted. Since no simple relationships are available for evaluation of radiation effects on seed production and reproduction potential, these "end points" were not used.

PREDICTION OF THE RADIATION EFFECTS IN THE ENTERPRISE FOREST

In the Brookhaven radiation forest, only lower plants (e.g., *Cladonia* and *Parmelia* sp.) survived radiation levels of 1000 r/day, whereas scattered, unhealthy tufts of *Carex pensylvanica* and isolated individuals of several other native herbs survived after 1 year of irradiation at exposures above 200 r/day (Woodwell and Rebuck, 1967). *Cladonia* and *Parmelia* sp., along with other lichens and mosses, are very common also in the Enterprise forest, and *Carex pensylvanica* is the most important and widely distributed herb, with a frequency of over 87% (Table 3). Other radioresistant genera, including *Rubus* sp. and several Ericaceae genera, are also present in the ground layer of both ecosystems (Woodwell and Sparrow, 1963; Woodwell and Rebuck, 1967; Tables 3 and 4).

Similarities also exist in the shrub layer of these two ecosystems. In the Brookhaven forest, three Ericaceae species survived at very high exposures (up to 160 r/day), and, although their lethal doses are not available, it seems that they may approach the 150 to 380 r/day predicted for this group of plants (Table 5). No information is available, however, for *Corylus cornuta*, which is the most important shrub of the Enterprise forest (Table 2) and whose nuclear characteristics (Table 5) indicate that it also should be one of the most radioresistant species, unless its upright form has some striking depressing effect.

Among trees native to the Brookhaven forest, *Quercus alba* and *Q. coccinea* mortality reached more than 90% at 110 r/day (Woodwell and Sparrow, 1963), with the 100% lethal dose approaching 170 r/day (Woodwell and Rebuck, 1967). This value agrees closely with the predicted lethal dose of 180 r/day for *Quercus rubra*, which has similar nuclear characteristics (Table 5). Finally, the similarity in nuclear characteristics between *Pinus rigida*, a dominant of the Brookhaven forest, and *Abies balsamea*, the most important gymnosperm of the Enterprise area, may be also reflected in their respective radiosensitivities, with an observed chronic lethal exposure of 23 r/day for the pine (Woodwell and Rebuck, 1967) and a predicted 28 r/day for the fir (Table 5). However, chronic irradiation (for one growing season) of planted *Abies balsamea* seedlings in our gamma field suggests that this species may be more radioresistant than predicted. Although no measurable shoot elongation took place in the season of irradiation, the lethal dose apparently was not reached, even at exposures of 43.2 r/day.

Table 5

RELATION BETWEEN INTERPHASE CHROMOSOME VOLUME (ICV) AND RADIOSENSITIVITY OF SOME PLANTS NATIVE TO NORTHERN ECOSYSTEMS

Species	Nuclear volume (NV), μ^3	Somatic* chromosome number (2n)	ICV, μ^3	Approximate daily exposure rate, r: Severe growth inhibition	LD_{50}†	Lethal‡
		Trees				
Abies balsamea	755	24	31.46	13	24	28
Larix laricina	1248	24	52.00	8	14	17
Picea glauca	1026	24	42.75	10	17	20
P. mariana	726	24	30.25	13	25	29
Acer rubrum	338	78	4.33	95	170	195
		104	3.25	125	225	260
A. saccharum	80	26	3.08	135	240	275
Betula papyrifera	203	56	3.62	110	205	235
		70	2.89	140	255	290
		84	2.41	170	305	350
Carpinus caroliniana	105	16	6.56	60	110	125
Fraxinus americana	99	46	2.15	190	340	390
Ostrya virginiana	42	16	2.63	155	280	320
Populus grandidentata	130	38	3.42	120	215	245
P. tremuloides	121	38	3.18	130	230	265
Prunus serotina	80	32	2.50	165	300	340
Quercus rubra	109	24	4.54	90	160	180
Tilia americana	127	82	1.55	265	480	540
		Other Woody Species				
Amelanchier (canadensis)§	133	68	1.95	210	380	440
Chamaedaphne caliculata	50	22	2.26	180	330	380
Cornus alternifolia	140	20	7.00	60	105	120
Corylus cornuta	43	28	1.54	270	480	540
Diervilla lonicera	90	18	5.00	85	150	170
Dirca palustris	147	38(?)	3.87	105	190	220
Ilex verticillata	131	36	3.64	110	205	235
Kalmia polifolia	143	44	3.28	125	225	260
		48	2.98	135	250	280
Ledum groenlandicum	150	26	5.77	75	130	150
Rubus allegheniensis	86	14	6.12	70	120	140
R. strigosus	80	14	5.50	75	135	155
		21	3.66	110	205	230
Vaccinium myrtilloides	72	24	3.01	135	245	280
		Herbaceous or Semiwoody Vegetation				
Aster macrophyllus	409	72	5.68	55		1080
Carex pensylvanica	92	36	2.55	120		2400
Cornus canadensis	117	44	2.66	115		2300
Gaultheria procumbens	89	24	3.71	80		1650
Lycopodium annotinum	304	68	4.47	65		1350
L. clavatum	184	68	2.70	110		2250
L. obscurum	154	68	2.26	135		2700
Maianthemum canadense	281	36	7.81	38		780
Mitchella repens	107	22	4.86	60		1250
Viola pallens	172	24	7.17	42		850

*From Darlington and Wylie (1956), and Ornduff (n.d.).
†Adapted from Sparrow et al. (1970), Fig. 5.
‡From Sparrow (1965), Figs. 4, 7, and 9.
§Tentative identification.

The similarities between certain species present at Brookhaven and species in the northern forest ecosystem facilitate the prediction of the radiation effects, but a comparison of the vegetation reveals striking differences in composition of all layers as well as in the richness of the flora. In the tree stratum, no field observation on radiosensitivity is available for most species that compose the northern forests. The predicted lethal values for angiosperm trees range from 125 r/day for *Carpinus caroliniana* to 540 r/day for *Tilia americana* (Table 5); these values agree closely with those for shrubs, which range from 120 r/day for *Cornus alternifolia* (the most radiosensitive) to 540 r/day for *Corylus cornuta* (the most radioresistant). This indicates that the zonation of both trees and shrubs should be similar unless other

Table 6

PREDICTED VEGETATION ZONATION AFTER A 5-MONTH GROWING-SEASON IRRADIATION WITH A 10,000-Ci SOURCE OF ^{137}Cs

Exposure,* r/day	Approximate distance from source,* m	Zone	Predicted surviving vegetation
1500	5	Devastated	No vegetation
500–1500	5–10	Lichen	Only lower plants; e.g., *Cladonia, Parmelia,* mosses
250–500	10–15	*Carex–Lycopodium*	Scattered individuals of *Carex pensylvanica, Lycopodium obscurum,* and perhaps *Cornus canadensis*
150–250	15–20	*Corylus*	*Corylus cornuta, Amelanchier* sp., and *Vaccinium myrtilloides* with seedlings and saplings of *Tilia americana, Fraxinus americana, Prunus serotina,* and *Ostrya virginiana*
65–150	20–30	Resistant angiosperm trees	*Tilia, Fraxinus, Prunus, Ostrya,* with some *Acer rubrum, A. saccharum, Betula papyrifera, Populus tremuloides, Quercus rubra,* and most original shrubs and herbs
20–65	30–50	Angiosperm trees	Essentially the original forest except gymnosperms (with occasional small trees of *Abies balsamea*)
20	50	Northern forest	Original northern forest

*Approximate exposure and distance are based on data by Woodwell and Sparrow (1963).

effects, such as the vegetation life form, will modify the predictions.

Effects of radiation on ground vegetation are the most difficult to predict from relationships between ICV's and radiosensitivity. The predicted lethal values are, in general, very high (Table 5) and may be unrealistically high in some instances. For example, the predicted value of 2400 r/day for *Carex pensylvanica* is far above the observed value of about 300 r/day (Woodwell and Oosting, 1965; Woodwell and Rebuck, 1967) in the Brookhaven radiation forest. The predicted lethal values in Table 5, which are from Sparrow's (1965) study with annual and perennial herbaceous seedlings exposed to gamma radiation for 8 to 12 weeks under favorable environmental conditions, may be considered as maxima obtainable for a given species. Our field prediction is based on a 5-month growing-season exposure of herbaceous vegetation composed only of perennial species with a high incidence of evergreen and semiwoody species. Moreover, the environmental stresses probably will reduce the lethal doses determined from ICV values, illustrated above with *Carex pensylvanica* and as follows from Woodwell and Oosting's (1965) study. They found only a few surviving herbaceous species at 1000 r/day and several more at 640 r/day in a second-year old field irradiated for one growing season, whereas the predicted lethal values for some of these species would range to more than 5000 r/day. Obviously some scaling factor must be used to adjust these lethal exposures for the harsher environment. A comparison of predicted with observed lethal exposures for the old-field vegetation indicates that the average ratio would be between 2 and 4, depending on whether the first- or second-year old-field data are used. Scaling the predicted lethal values (Table 5) by this factor would bring the levels for the most radiosensitive herbs, such as *Maianthemum, Viola, Aster,* and *Mitchella,* within the range for woody species, but resistant species, such as *Lycopodium obscurum, L. clavatum, Carex pensylvanica,* and *Cornus canadensis,* would still remain the most radioresistant higher plants of the northern forest ecosystems.

The prediction of vegetation zonation after a 5-month growing-season exposure is presented in Table 6 for the most important woody species and several widely distributed herbs. The zones are named for important species expected to survive the incident exposure, although their populations may be drastically reduced and their growth severely inhibited. For example, the 250- to 500-r/day zone (approximately 10 to 15 m from the source) is the *Carex–Lycopodium* zone because some individuals of these species are likely to survive in it; however, these two species should develop better and perhaps even benefit from selective removal of the more radiosensitive species in the next zone (150 to 250 r/day), which is designated the *Corylus* zone. Shielding by tree trunks, rocks, and topography is likely to produce additional local changes in the vegetation pattern, but these should be of minor importance on an area basis.

Although the ionizing radiation will be directly and solely responsible for the early changes in vegetation composition and structure, the resultant indirect effects should become more pronounced with time and eventually may be more important in the recovery of the community and the development of the vegetation in subsequent years. The severely damaged portions of the northern hardwood and birch forest types probably will revert to earlier successional stages featuring some native light-tolerant species such as *Pteridium aquilinum* and *Fragaria,* as well as introduced light-seeded species such as *Aster umbellatus, Chrysanthemum leucanthemum, Juncus tenuis, Achillea millefolium,* and some grasses.

At intermediate exposures where the radiosensitive species will be selectively eliminated and others severely suppressed, the radioresistant species should

benefit from the decreased competition. Among herbs, *Carex pensylvanica* is likely to increase its cover at exposures between 40 and 250 r/day, as it did in the Brookhaven forest (Woodwell and Rebuck, 1967). Between 40 and 150 r/day, cover of *Corylus cornuta* along with some Ericaceae shrubs may increase, and the removal of radiosensitive tree species may help *Tilia, Ostrya, Prunus,* and *Fraxinus* by increasing their available growing space. These changes probably will take place during the radiation treatment and may continue for some time after the treatment before the recovery of damaged trees becomes significant.

The recovery of both devastated and severely damaged areas may be rapid because of the high sprouting potential of most woody species and many perennial herb species native to northern forests. Sprouting is an important mechanism of recovery after logging or mechanical destruction and probably will be the main mechanism after irradiation destruction, as was reported for a mixed pine–hardwood forest in Georgia by Cotter and McGinnis (1965). In areas where it occurs, aspen is likely to assume a prominent role in regeneration of radiation-devastated areas because it sprouts profusely from the roots, which are protected from radiation damage by an effective shield of soil. Possible genotypic variation in radiosensitivity or sproutability may favor certain clones in recovery from radiation damage. Other angiosperm genera, such as *Tilia, Acer,* and *Quercus,* sprout from stumps or from living portions of trees with dead crowns. Compared with root sprouts of aspen, which may occur at higher exposures than stump sprouts and are likely to increase the total area covered by aspen, these stump and stem sprouts are spatially restricted but will contribute to the recovery of partially affected portions of the forest.

Although recovery of the radiation-damaged forest will be mostly by sprouts, tree species with light, wind-disseminated seeds, such as aspen and birch, may provide some seedling regeneration. However, seedlings may be hindered by competition from the native radio-resistant herbaceous vegetation that is likely to increase in the first year after irradiation. Viable seeds of woody species are also present in the soil, which may protect them from serious radiation damage and allow them to germinate and contribute significantly to the recovery.

The complexity and floristic richness of the northern forests indicate that many other patterns of recovery can be expected, especially in bogs, which have heavy mats of mosses, ferns, and sedges, and on the road, which has many introduced annuals and perennials found mostly in disturbed areas. Because information on the radiosensitivity of these species is inadequate, no attempt is made to predict radiation effects on this vegetation and its postirradiation recovery.

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Table A-1

RELATION OF INTERPHASE CHROMOSOME VOLUME (ICV) AND RADIOSENSITIVITY OF SOME NATIVE AND INTRODUCED HERBACEOUS PLANTS

Species	Nuclear volume (NV), μ^3	Somatic chromosome number (2n)	ICV, μ^3	Approximate daily exposure range, r: Severe growth inhibition	Approximate daily exposure range, r: Lethal
Achillea millefolium	248	54*	4.59	65	1350
		18	13.78	22	450
		36	6.89	44	900
		72	3.44	87	1800
Aralia nudicaulis	100	24	4.17	72	1480
Aster ciliolatus	238	72	3.31	91	1870
A. umbellatus	110	18	6.11	49	1010
Athyrium filix-femina	500	80*	6.25	48	990
		60	8.33	36	740
		100	5.00	60	1240
Clintonia borealis	885	32*	27.66	11	225
		28	31.61	9	195
Chrysanthemum leucanthemum	225	36*	6.25	48	990
		18	12.50	24	500
		42	5.36	56	1150
Erigeron annuus	112	27	4.15	72	1490
Galium triflorum	93	44*	2.11	142	2930
		22	4.23	71	1460
Hieracium aurantiacum	154	30	5.13	59	1200
		45	3.42	88	1800
Luzula acuminata	61	48	1.27	237	4880
Plantago major	83	12*	6.92	43	900
		24	3.46	87	1790
Pyrola rotundifolia	277	46	6.02	50	1030
P. virens	212	46	4.61	65	1340
Solidago sp.	158	18*	8.78	34	710
		36	4.39	68	1410
		54	2.93	102	2110
		60	2.63	114	2350
Streptopus roseus	272	16	17.00	18	365
Trifolium repens	89	32*	2.78	108	2230
		48	1.85	162	3350
		64	1.39	216	4460
Viola incognita	172	44	3.91	77	1580

*Chromosome number most frequently cited in the literature.

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ADDENDUM

Since this paper was prepared early in 1971, nuclear characteristics (nuclear volume, interphase chromosome volume, and somatic chromosome number) were determined and radiosensitivity values were calculated for additional important herbaceous species of the Enterprise Radiation Forest (Table A-1). New maximum and minimum ICV's found in this group of plants suggest that the range in radiosensitivity among the herbaceous species will be greater than previously predicted. That the ICV of *Luzula acuminata* (1.27 μ^3) was the lowest for all plants so far analyzed indicates that this member of the rush family may be the most radioresistant. At the other extreme, the ICV of *Clintonia borealis* was estimated at 27.66 μ^3, which is by far the highest among broadleaf species and approaches the ICV's of coniferous species. *Clintonia borealis* has large fleshy leaves that rise only about 5 to 10 cm above the ground. This low growth form, as well as the high water content, make radiosensitivity prediction difficult, but it is expected that this species will be among the most sensitive herbs.

ICV determinations and radiosensitivity predictions for several herbs of the logging-road community were hampered by lack of reliable data on somatic chromosome numbers. More than one somatic chromosome number appears in the literature for *Achillea millefolium, Chrysanthemum leucanthemum, Galium triflorum, Hieracium aurantiacum, Plantago major, Solidago* sp., and *Trifolium repens.* These reported somatic chromosome numbers cover a wide range of values; these are also reflected in the predicted radiosensitivity data. The same problem was encountered in such previously discussed woody species as paper birch, red maple, and raspberry (*Rubus strigosus*). We will attempt to verify the chromosome number in populations of these species found in the Enterprise Radiation Forest before evaluating the accuracy of the predictions.

The ICV range was much wider and the mean was larger for herbaceous plants

found under canopies of the forest types than for plants of the logging-road community, but the means (6.58 and 4.91 μ^3, respectively) were not significantly different. The overall mean ICV of 27 herbaceous or semiwoody species listed in Tables 5 and A-1 was 5.84 μ^3.

The predicted radiosensitivities will be compared with the actual radiosensitivity observed and measured during and following the 1972 growing-season radiation exposure.

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HOWARD T. ODUM, Editor and Project Director
University of North Carolina, Chapel Hill, North Carolina

ROBERT F. PIGEON, Associate Editor
Division of Technical Information, U. S. Atomic Energy Commission, Washington, D. C.

An intensive ecological study of several hectares of montane rain forest was made during the 1960s in the Luquillo National Forest in eastern Puerto Rico. The operation of the normal forest was studied and compared with a zone that for three months received gamma-radiation stress from a 10,000-curie cesium source that had been airlifted into the forest. The book reports the scientific results of the project, which used many techniques of systems ecology in the quest of understanding one of the most complex ecosystems on earth. Included in nine main divisions (111 chapters) are maps, tables of tree numbers, and taxonomic keys to facilitate new efforts at the El Verde site toward finding the best designs for man and nature in broad tropic lands.

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